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In celebration of Ivo Hodek's seventieth year

This year, Ivo Hodek achieves his seventieth birthday. It seems hardly credible for those of us who have known him for most of his exciting scientific and social career. Before describing his internationally recognized contribution to entomology we shall present a short account of his career.

Ivo was born on June 3, 1931 in Prague, the only child of a bank clerk. Ivo finished his high school studies in 1950 and immediately began his University Studies in the Faculty of Agronomy of the College of Agriculture, in Prague. In the following year he entered the Faculty of Science of Charles University, Prague, where he continued his studies in zoology. Under Professor Julius Komárek of the Institute of General Zoology Ivo specialised in entomology. He finished his studies in 1954 by defending his thesis on the ecology of the ladybird beetle, *Coccinella septempunctata*. The biology of coccinellids was his main love for many years. In 1957, he finished his PhD Thesis, also on the ecology of *C. septempunctata*, at the Entomological Institute of the Czechoslovak Academy of Sciences, where he then started what was to be a life-long and highly successful career. He occupied the position of research scientist from 1957–1964, and senior research scientist from 1964–1974, first in his beloved Prague and then České Budějovice. In 1966 he was awarded the RNDr degree by the Faculty of Science of Charles University, which for administrative reasons was long after he had finished the study that led to this award. Between 1974 and 1997 he was one of the top ranking scientists in the Academy of Sciences, i.e., an outstanding research scientist and a now well established international expert. In 1997 he was made an emeritus research scientist. From 1990–1998 he was the Head of the Laboratory of Ecophysiology, a research group that he created in 1989.

Ivo Hodek was the founder of experimental insect ecophysiology in the Czech Republic. He worked mostly with two insect groups, ladybird beetles of the family Coccinellidae, mainly *Semiadalia undecimnotata* and *Coccinella septempunctata*, and, heteropteran bugs of the families Pyrrhocoridae, *Pyrrhocoris apterus*, and Pentatomidae, *Aelia acuminata*, *Dolycoris baccarum* and several other species. The breadth of ecophysiological problems studied using these few species was, however, wide. The full extent of his interests is well illustrated by the huge diversity of subjects included in his list of publications. Here we shall comment only on his more outstanding contributions. His initial studies were on the effect of plant allelochemicals, sequestered by phytophagous prey, on insect predators. The phytophagous prey was the aphid, *Aphis sambuci*, which is toxic to the coccinellid predator, *C. septempunctata*, because of the alkaloids and glycosides it ingests from its host plant, *Sambucus nigra*. This research stimulated further activity and similar allelochemical effects were demonstrated in other aphidophagous predators, chrysopids (Neuroptera) and syrphids (Diptera). Ivo's studies on aphidophagous insects concluded with the publication of an influential book, Biology of Coccinellidae (1964) whose second edition, Ecology of Coccinellidae, appeared in 1996.

Early in his study of the trophic biology of aphidophagous coccinellids Ivo branched into the study of the ecophysiology of insect dormancy. This was done initially on the coccinellid, *Semia-*

dalia undecimnotata. Later he became engrossed with the effects of photoperiod and temperature on adult diapause, mainly in several heteropteran species, and challenged some widely accepted generalisations concerning the effect of chilling and daylength on the termination of dormancy. Among his most fascinating achievements was the demonstration that sensitivity to daylength in adults of *Pyrrhocoris apterus* gradually reappeared when the diapause was terminated by chilling. The climax of his dormancy studies came when he proposed his theory of multiple pathways of diapause completion. A diapausing individual may switch, depending on environmental conditions, between different processes of diapause termination with two extremes: slow "horotelic" processes (e.g. those caused by chilling) and fast "tachytellic" processes (e.g. processes caused by photoperiodic stimulation). Adopting different processes affects postdiapause performance, including the sensitivity to re-induction of dormancy. Of course, many other exciting contributions may be found in Ivo's many papers on dormancy. These are only a few highlights of Ivo's many achievements.

Ivos scientific work was always accompanied by intense social activity. The most significant was the organisation of symposia, some of which became established periodical opportunities for international scientific communities to meet. Of theses perhaps the most important was the very successful "Aphidophaga" Symposia the first of which (Ecology of aphidophagous Insects) was held in 1965, at Liblice (Czechoslovakia), the second (Ecology of Aphdophaga) in 1984 at Zvíkovské Podhradí (Czechoslovakia). Subsequent symposia in this series were held at much shorter intervals in several countries including Poland, Hungary, France, Belgium and Canada. Of equal importance was his role in organizing the first Symposium on Insect Ecophysiology. This was the French-Czech Symposium Diapause et Voltinisme held in Prague in 1974. The Second European Workshop on Invertebrate Ecophysiology was held at České Budějovice, in 1995.

Ivo has also devoted much energy to his editorial activities. Since 1986 Ivo has been a member of the Editorial Board and the Executive Editor of the European Journal of Entomology, formerly Acta Entomologica Bohemoslovaca. His editorial and reviewing ability were equally appreciated by the Editors of other Journals who invited him to serve on their Editorial Boards: Entomologia Experimentalis et Applicata, Entomophaga, Biocontrol Science and Technology, Ekologia Polska, Acta Societatis Zoologicae Bohemicae.

Significant too is Ivo's contribution as a teacher. Paradoxically he first taught when doing research at foreign Universities: in 1972–1973 at the University of Wageningen (The Netherlands), and in 1979–1980 at the F. Rabelais University in Tours (France). In 1991, he was appointed External Reader in Ecophysiology in the Faculty of Science at Charles University, Prague, and in 1995 Lecturer in the Faculty of Biological Sciences, University of South Bohemia, České Budejovice.

He is a member of numerous Scientific Societies, where his most important duty was that of Librarian to the Czechoslovak Entomological Society and the Czechoslovak Zoological Society, which task he fulfilled for many years. He had a significant influence on the number of periodicals exchanged by the libraries of both Societies. Ivo's life long achievement was acknowledged and honoured by the Jan Evangelista Purkyně Medal awarded him by the Academy of Sciences of the Czech Republic in 2000.

We conclude this short enumeration of Ivo's activities and modest evaluation of the significance of his achievements, the results of nearly 50 years of fruitfull scientific activity, by hoping he will long continue to provide significant contributions to international science. We wish him much success and vitality, not only in his professional career, but also in his personal life.

Karel Hůrka & Alois Honěk

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Long rather than short diapause-promoting photoperiods induce strong diapause in green lacewings (Neuroptera: Chrysopidae)

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Abstract. Two west-Palaearctic green lacewings, *Nineta pallida* (Schneider, 1846) and *Dichochrysa picteti* (McLachlan, 1880), overwinter as free-living larvae. The longest photoperiod that induced whole populations to enter diapause is that occurring at the time of the equinox, the so-called intermediate days, also induced the strongest responses. These are differences in the duration of horotelic-processed development, and in their ability to resume morphogenesis spontaneously without stimulation. That is, there is evidence of multiple diapause-promoting daylength regimes. The term **constraining photoperiod** is proposed for photoperiods that produce the most intense diapause. The adaptive value of the above relation is that synchronizes the life cycles of individuals within a population: intermediate photoperiods in the field coincide with the early induction of diapause, which lasts for longer. Synchronization of the life cycle was secured by a non-reversable developmental arrest of some individuals, the proportion of which was higher under the constraining photoperiod than under shorter days.

Photoperiod, diapause, diapause intensity, life-cycle regulation, Neuroptera, Chrysopidae, Nineta pallida, Dichochrysa picteti, Palaearctic region

INTRODUCTION

On land, in temperate climates, periods that are favourable for development of insects usually alternate with unfavourable cold or dry periods. Many insects use the light-and-dark diel cycle (photoperiod) as a signal heralding the arrival of the unfavourable periods and thereby to synchronize in time and space the feeding stages with food availability. To avoid freezing and starvation, they migrate or enter a condition of arrested development called dormancy, quiescence or diapause.

Thus the incidence of diapause depends on photoperiod; a critical photoperiod is an estimate of the population's mean photoperiodic response threshold (Beck 1980) and is that at which 50% of a population enter diapause in a given ecological situation. This produces a sharp change in the developmental pattern, in particular the occurrence of diapause (seasonal adaptation) and in phenology (biotope possession). The more variable (i.e. northerly) is the photoperiod, the more it is easy to detect and the stronger its effects in regulating the yearly life history.

Morphogenesis is resumed after completion of physiological processes that have been termed by Hodek (1981) horotelic or tachytelic if after stimulation they proceed at a "normal" or a faster rate, respectively. Ability to resume morphogenesis spontaneously under diapause-inducing conditions is not an intrinsic generalized character in lacewings; such a lack of development resulting in death under laboratory conditions was previously termed "ately" (Canard & Grimal 1993).

The response to photoperiod may be a more or less intense. The intensity of diapause may be recorded, although this characteristic is not easy to outline (Principi 1992). Some measurable parameters are available, each of them only depicting a single facet and giving a partial idea on the depth of the diapause:

- the incidence of diapause induction, if not an all-or-nothing response;
- the duration of diapause under steady inducing and maintaining conditions, if spontaneous termination is possible;
- the rate of resumption of development;
- the duration of survival of the individuals that die without resuming morphogenesis;
- the decrease in metabolic activities such as O_2 consumption, heart beat frequency;
- the reduction in consumption of reserves reflected in weight loss during diapause, or changes in fat content;
- the casual appearance of prolonged diapause, if more than one full year is needed to complete this life-cycle.

Over the past 25 years, chrysopids have yielded much information on diapause, especially on the role of photoperiod in their life-cycle. Several species show the classical photoperiodic responses I and II of Beck's classification (1980), but some others manifest more or less sophisticated diapause mechanisms (Canard 1998). This diversity raises the question: do the longer diapause-promoting daylengths induce stronger diapause than the very short ones? Some green lacewings may provide a tentative answer.

MATERIALS AND METHODS

Dichochrysa picteti (McLachlan, 1880) is a multivoltine Atlanto-Mediterranean species occurring between latitudes 30 and 45 °N. *Nineta pallida* (Schneider, 1846) is univoltine; it occurs in Central Europe as far north as 55 °N, and lives as isolated populations in montane habitats, as far south as 43 °N. The two strains studied originated from southern France. They both overwinter as larvae that hatch from eggs laid in late summer and/or autumn (Canard 1990, Canard et al. 1991). The seasonal synchronisation of their life cycle depends on the actual timing of the overwintering generation, and on diapause mechanisms (Canard et al. 1992). Embryos and early larval instars are sensitive and responsive to external cues (Canard 1990, Canard et al. 1991). The duration of the larval instars is long compared to that of many other chrysopids; *N. pallida* in its single annual generation, and *D. picteti* at least in the overwintering generation. Consequently, the relevant larvae are exposed to a wide range of daylengths including diapause-inducing ones.

In the laboratory the larvae were reared under the following conditions: temperature 21 ± 1 °C, relative humidity from 60 to 80 %, light intensity less than 500 lux into the vials, food consisted of the pea aphid *Acyrthosiphon pisum* (Harris, 1776) and sterilized eggs of the Mediterranean flour moth *Anagasta kuehniella* (Zeller, 1879). They were subjected to photoperiods, which simulated the light regimes the target chrysopids encountered under natural conditions in the more northern part of their distribution. The larvae were kept singly and observed daily. Of the parameters for quantifying diapause intensity there are listed above, only the first four were analysed.

RESULTS AND DISCUSSION

The incidence of diapause induction showed (Fig. 1) that the response to daylength as an all-or-nothing reaction: diapause vs non-diapause, namely continuous fast growth vs a slow down (or break) in development. The curves of the responses to daylength, in hours of light per day (= h/d) equal or longer than 6 hours in *Nineta pallida* and 8 hours in *Dichochrysa picteti* indicate a long-day type of photoperiodic response according to Beck which was very similar in the two species. They only differ in the values of the threshold photoperiod, which was about 14:30 h/d in *N. pallida* and 15:15 h/d in *D. picteti*. This does not suggest a peculiar diel rhythm. A premature conclusion might conceal other aspects of the mechanism of diapause induction.

Diapause development, in the first- (*N. pallida*) and third- (*D. picteti*) stages (Fig. 2), differed in a range of diapause-inducing conditions. Of the interpretations, one is that the difference in the horotelic processes is affected by daylength. The two species displayed the same general strategy: (i) the longest duration of diapause occured at the intermediate day-lengtha, namely 12 and 13 h/d in *N. pallida* and *D. picteti*; respectively; (ii) all diapause-averting photoperiods (long days) produced homogeneous tachytelic responses, (iii) and diapause-inducing daylengths (intermediate and very short days) produced random responses; (iv) the most heterogeneous response was recorded under intermediate day-lengths.

The resumption of morphogenesis generally did not occur spontaneously: in the two species some individuals did not emerge from diapause under the constant photoperiods used (Fig. 3). In *N. pallida*, all the larvae started to develop and reached the first ecdysis, except when the photoperiod was 12 h/d, when about 20 % of them died after 42 to 94 days [x = 63.3 ± 17.3 (S. D.)] without moulting. These larvae were in the irreversible diapause condition termed ately. They probably need the stimulation of a period of tachytelic processes. In *D. picteti*, all conditions leading to horotely permanently inhibited a large part of the larval population. However, ately was highest at photoperiod of 14 h/d when 70 % of the larvae failed to resume growth and died. Increasing daylengths may play a stimulating role (Canard et al. 1991).

The duration of survival of the atelic *D. picteti* larvae ranged from 32 to 110 days. The results were very variable (coefficients of variation from 0.12 to 0.25), so the analysis did not reveal any significant differences. In this case, duration of survival of atelic larvae was not a good parameter for estimating diapause intensity.

In natural conditions, this strategy effectively synchronizes the wintering brood, and thus regulates the life-cycle. Intermediate daylengths correspond in the field with the early induction of strong diapause and a longer larval diapause, and the very short days responsible for the late induction of diapause. The earlier (late summer or autumn) the diapause induction, the deeper the subsequent diapause and the slower the diapause development, so that the emergence from dia-

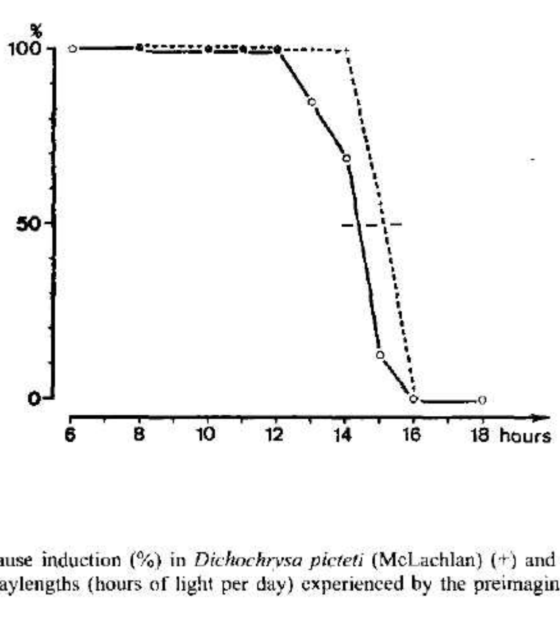

Fig. 1. Incidence of diapause induction (%) in *Dichochrysa picteti* (McLachlan) (+) and *Nineta pallida* (Schneider) (o) as a function of the daylengths (hours of light per day) experienced by the preimaginal instars in the laboratory.

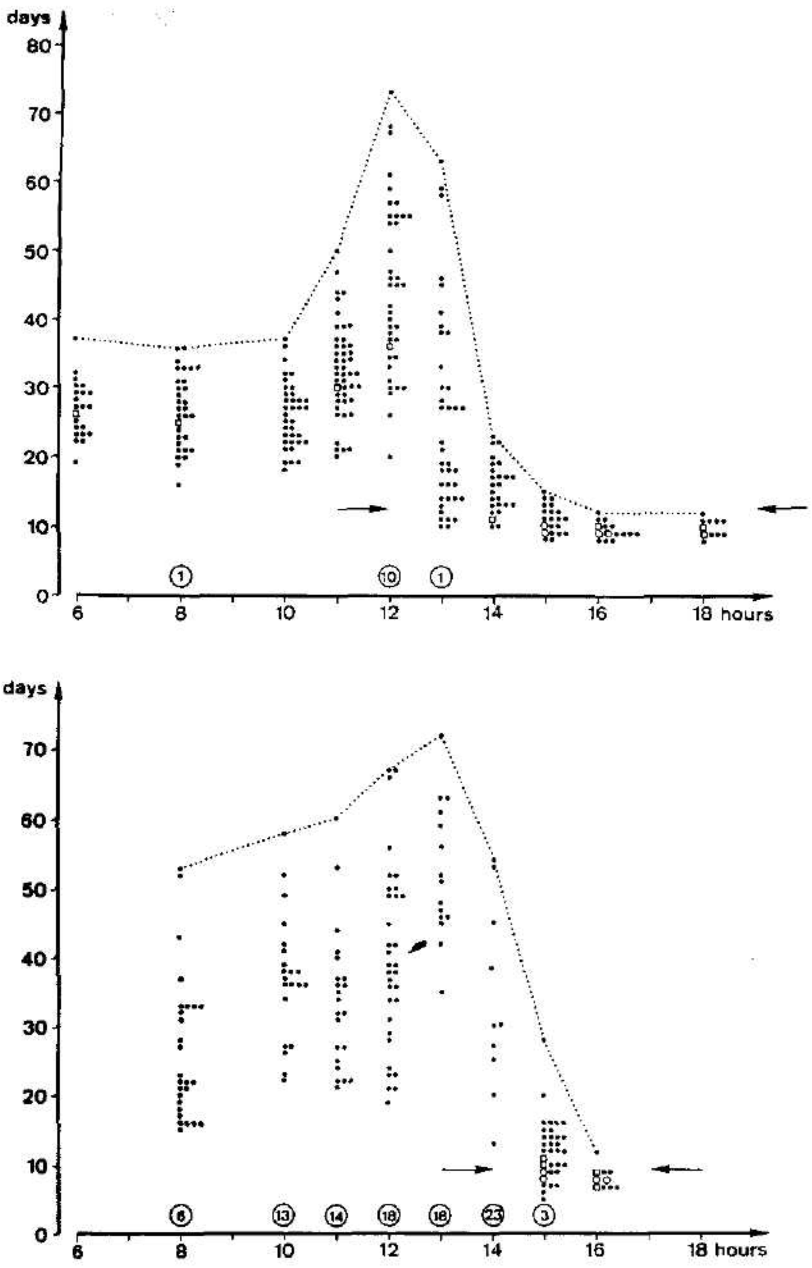

Fig. 2. Duration in days of the diapause of larvae as a function of daylength. Above = first instar *Nineta pallida* (Schneider). Below = third instar *Dichochrysa picteti* (McLachlan). Open circles represent 10 individuals, open squares represent 5 individuals, solid circles represent 1 individual; rounded figures are the numbers of dead specimens. The arrows indicate the times beyond which diapause was considered to occurr.

pause will be delayed. This relation is, of course, valid only within the range of diapause inducing photoperiods (Fig. 1). Conversely, the later (late autumn or winter) the diapause induction, the weaker the diapause and faster the diapause development. Diapauses of larvae, which may in winter be partially active, must be strictly controlled by environmental cue(s) to avoid resumption of development, especially in mild winters. Locking up the life-cycle course was complementarily secured by a non-reversable break in the development of some individuals in the absence of reactivating signals; the rate of standing by arrested larvae was higher under constraining photoperiods than under shorter days.

Similar reactions have been reported in other insects, for example, in the diapausing pupae of the tobacco hornworm (Bell et al. 1975), in the common carnivorous midge (Havelka 1980), and in the alydid Japanese bean bug (Nakamura & Numata 2000). In the last species, which diapauses as an adult, the different photoperiods have a quantitative affect on both the initial intensity of diapause and the rate of diapause development. In the chrysopids, such an action has been foreshadowed in the common green lacewing, *Chrysoperla carnea* (Stephens, 1836) sensu lato, a species that exhibits reproductive photomediated diapause and manifests a reduced winter activity (Sheldon & MacLeod 1971); Hodek &Honek (1976) demonstrated, in a European strain that late autumn and winter photoperiods (very short days) – if perceived what it is cold – neither prolonged nor maintained diapause. On the contrary, Tauber &Tauber (1972) suggested that the two closely related strains of *Chrysoperla plorabunda* (Fitch, 1855) (as the North American "*Chrysopa carnea*") show a graded response to daylength: the depth of diapause (duration) varies as a function of daylength from 8 to 13:30 h/d in the New York strain and 8 to 12:30 h/d in the Arizona strain. In *Chrysoperla harrisii* (Fitch, 1855), diapause-inducing daylengths near the critical photoperiod produce weaker diapause than day-lengths shorter than the critical photoperiod (Tauber & Tauber 1974).

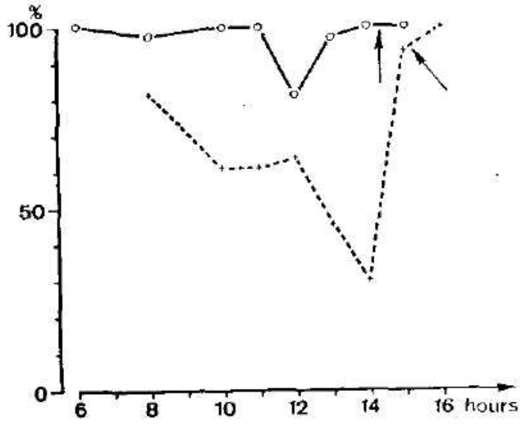

Fig. 3. Incidence of spontaneous resumption of diapause (%) in *Dichochrysa picteti* (McLachlan) (+) and morphogenesis in *Nineta pallida* (Schneider) (o) as a function of the daylengths under which the diapausing third-instar larvae of *D. picteti* and first-instar larvae of *N. pallida* were kept. The arrows indicate the respective critical photoperiods.

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The nature of dormancy responses in insects

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Abstract. This paper takes a deliberately broad view of the ultimate purposes, the structures and the controls of dormancy responses in insects. Dormancies have multiple purposes (Tab. 1); in particular, they serve not only to survive adverse seasons but also to ensure that activity and development take place at favourable times of year. Many elements can contribute to the structure of the responses (Tab. 3) including different types and different extents of delay, control, sensitivity, default conditions, components, pathways and variability. Control options come from a range of internal and external factors (Tab. 4). The multiplicity, complexity and integration of the various facets of dormancy confirm that responses are dynamic and hence are by no means equivalent to simple on-off devices. Consequently, dormancy responses are best understood by considering whole life cycles in the context of whole environments, normally requiring studies that go beyond the simple approaches that are still prevalent.

Dormancy, diapause, response, trade-off, variability, life cycles, Insecta

INTRODUCTION

The majority of insects can slow down their development below the maximum rate that is possible under any particular combination of temperature and other conditions. The most marked example of such delayed development is the complete cessation of normal activity for long periods during "classical" instances of diapause. Here I include in the category of "dormancy responses" not only classical diapause but also much less marked modifications of development. Such modifications are very common, reflecting the fact that development can be manipulated or optimized in a remarkable range of ways.

Three facets of dormancy allow these responses to be understood: the purpose or target of developmental delays, which reflects ultimate environmental requirements; how dormancies are structured into the life cycle; and the internal and external elements of control. This paper enumerates key aspects of each of these three facets. Such a broad approach to summarizing components of the response from different perspectives provides insights into the complexity of dormancy and its proper study. Relatively few references are cited for illustration, because many specific examples can be found in earlier reviews (e.g., Danks 1987, 1994a).

PURPOSES OF DORMANCY RESPONSES

Roles of dormancy

Dormancies enhance survival not just by providing a means to stop development in a stage that can withstand adversity, but also by ensuring that development or reproduction will coincide with favourable conditions (Danks 1987, Williams 1998). Examples of life-cycle requirements of this sort that can be met by dormancy responses are shown in Tab. 1. Many species enter winter dormancy

Tab. 1. Examples of life-cycle requirements that can be met by dormancy responses

requirement and sample constraint	sample response
survive or avoid adversity	
cold	winter diapause in cold-hardy stage; prolonged development to prevent appearance of cold-susceptible stage
dryness	summer diapause in desiccation-resistant stage
other	larval diapause during peak period of parasitoid activity; larval diapause when foodplants are unavailable or inedible
coincide development with favourable or optimal conditions	
physical conditions	larval growth only in the warm spring
resources	egg hatch (after diapause) coincides with bud burst
coincide reproduction with favourable or optimal conditions	
physical conditions	oviposition restricted to midsummer
resources	appearance of adults coincides with availability of oviposition sites and of nectar plants to support reproducing adults

in a cold-hardy state (Denlinger 1991). Other species prolong development at certain times of year, to ensure that an inactive stage need not endure for many weeks before the adverse season, requiring additional energy or resistance, or to ensure that a vulnerable stage will not appear before or during the adverse season (e.g., Goettel & Philogène 1978, Grüner & Masaki 1994, Papadopoulos et al. 1998). Similar features are well known in response to summer drought (Masaki 1980, Harada 1998, Williams 1998). Dormancies may respond to other factors that threaten survival, such as the attack of predators or parasitoids (Kukal & Kevan 1987), the absence of prey (Zaslavsky et al. 1999) or the absence of food plants (many species).

Many studies of dormancy have emphasized such passive or defensive timing against adversity. However, adjustments of development for active coincidence with potential benefits is equally common. For example, diapause may structure the life cycle to ensure that larval growth occurs at an optimal time for juvenile survival (Leinaas 1983), or to synchronize the life cycle with bud burst (many tree-feeding moths in spring), with young food plants or hosts (many species of different orders), and so on. Similar coincidence is important for reproduction, because oviposition may be restricted to times of year with temperatures optimal for female activity or egg development (Corbet & Danks 1975), or to periods when oviposition sites and nectar plants are available.

The greatest difficulty in understanding the value of all of these responses is that "obvious" assumptions may be erroneous. The most important selective factor may be less visible than some more striking factor that is merely correlated with or coincides with the dormancy. For example, some high-arctic caterpillars cease development relatively early and overwinter on ridges fully exposed to bitter cold, but this overwintering site allows for the earliest possible start in spring, an especially important requirement at high latitudes because the summer is so short (Danks 1981, 1993). In other words, ensuring development at cool summer temperatures is more critical than avoiding very cold winter temperatures.

Multiple factors

Life cycles therefore reflect integrated responses to many rather than single factors. One way to interpret such multiple responses is to analyse environments in terms of the three core elements that enable them to support life, the factors of time, space and energy (cf. Danks 1987, 1993, 1994b, 1999), and thus in terms of seasonality, habitats and their heterogeneity, and other resources.

Although the factors interact, because a given species depends on food energy at a given time in a given place, listing these components in more detail (Tab. 2) is helpful for considering selective forces.

Trade-offs and complexity

Another way to assess the contributions of multiple factors as well as their integration is by analyzing trade-offs. Such analyses have generated considerable literature, reviewed in general terms by Roff (1992) and Stearns (1992). Components that can be traded off, and some more detailed sample comparisons, are given by Danks (1994a). They include such energy trade-offs in larvae as dormancy, size, rate of development, food storage, resistance to adversity and dormant metabolism, and in adult females as morph, size, reproductive effort (and in relation to stored reserves), fertility, fecundity, clutch size, egg size and adult feeding, as well as delayed reproduction through domancy or dispersal. Intraspecific comparisons are most informative.

Many instructive trade-offs have been reported. Well known examples related to dormancy include especially growth rate and diapause, and other recent examples include rapid development versus resistance to adversity (Borash et al. 1998), diapause maintenance versus reproduction (Ishihara & Shimada 1995, Kroon & Veenendal 1998), small size versus diapause (Saunders 1997) and rate of development versus fecundity (Karban 1997). Most work compares pairs of attributes expected to trade off, but in real situations many and not just two factors trade off simultaneously, and also the key components of a single trait are themselves complex. For example, the several different elements that contribute to realized fecundity are not necessarily genetically integrated (cf. Stirling et al. 1999). Traits such as growth rate and development time that normally are correlated can be adjusted separately in some species (Blanckenhorn 1997b). Therefore, it is very difficult to establish "rules" for the trade-offs, and nor does modelling usually provide clear-cut answers.

Serial trade-offs through the life cycle are important. For example, Schneider (1996) supposed that the small eggs of the spider *Stegodyphus lineatus* Latreille, 1817 allowed fast development, thereby reducing the serious risk of egg parasitism by producing mobile spiderlings that could readily disperse. Complexity is enhanced by the effects of habitat structure, notably differences in selection for reproductive and other traits depending on the scale and heterogeneity of habitats (Statzner et al. 1997), and whether predictable refuge habitats to maintain the population exist in addition to ephemeral ones (Wissinger 1997).

Tab. 2. Some environmental elements relevant to dormancy responses

category	element	sample response
time	season permitting survival	timing of resistant stages
	season permitting growth	rate of growth; final size
	season permitting reproduction	reproductive dormancy; onset of emergence; duration of reproductive period; pattern of oviposition
	duration of suitable habitat	dispersal; dormancy in situ; refuge habitats
space	suitable habitats elsewhere	dispersal
	safer habitats elsewhere	dispersal and dormancy
	suitable but different habitats elsewhere	geographic differences in life cycle
energy	heat resources (e.g., seasonal heat sum)	favoured habitats; favoured seasons (see above); basking and other behaviour
	food resources	specialist or generalist feeding; coincidence with limited feeding periods; dormancy in immediately pre-feeding stage

Finally, the trade-offs that might be expected are not inevitable. For example, size and time need not be traded off if time is not limiting because growth ends well before the end of the favourable season (review by Danks 1994b).

Attempts to assess the ultimate purposes of dormancy responses therefore provide two major lessons: there is more than one way, including a range of types of dormancy, to reach the same "adaptive" objectives; and responses are integrated in a complex way over the whole life cycle. Insights are therefore more likely to come from well planned multifaceted experiments on single species than from scattered comparisons of pairs of factors that might be traded off, such as developmental rate and size.

STRUCTURE OF DORMANCY RESPONSES IN THE LIFE CYCLE

Life cycles can be structured in a very wide range of ways. Here I take the broadest view of the structure of dormancy responses, rather than treating details applicable to individual species such as stage, seasonal placement or voltinism. (For a summary of the detailed components, see Danks 1994a: tab. 3.)

The broad elements are summarized in Tab. 3. Further information on each element is given below.

Default starting-response

Either development or dormancy is the normal default response at a given stage of development, so that the alternative has to be specifically signalled or induced (Danks 1987: 16). Thus an absence of alternative signals either ensures that "obligate" diapause will begin (e.g., reproductive diapause at constant temperature in *Hypogastrura tullbergi* (Schäffer, 1900): Birkemoe & Leinaas 1999), or that development will continue (the majority of species, in which diapause is induced only if particular cues are received). Which alternative is advantageous depends chiefly on the nature of environmental risks: for example, obligate delays protect against environmental signals that might be misleading; active responses allow full use to be made of environmental information that is likely to be helpful.

Type of response

Dormancy ranges from a single, fixed delay (such as an arrest in development) to continuous responses such as modified larval growth the rate of which at any time depends on current seasonal tokens. Such plastic responses or "state-dependent decision processes" (Gotthard et al. 1999) provide great developmental flexibility. They have been best characterized in some species of Lepidoptera (e.g., Nylin 1994) but are known in many other species. Of course, both fixed (all or none) and plastic (graded) responses can occur during the same stage (Tanaka et al. 1999).

Plasticity is advantageous especially when the favourability of environments changes in the short term, so that a fixed response might prove inappropriate. Plasticity is also necessary when habitats are heterogeneous on a small scale (cf. Sakwinska 1997), or when gene flow would prevent selection on a larger scale (e.g., Blackenhorn 1997a). In such circumstances, only general timing patterns that can be modified by short-term local responses, and not more precise local genetic adaptations, are feasible.

Type of delay

Possible responses range from minor reductions in growth rate to complete and lengthy diapauses. Changes in growth rate, commonly cued by factors such as photoperiod, may be accompanied by other life-cycle changes, for example in the numbers of instars, as reported for species in a wide range of insect orders (e.g., Fantinou et al. 1996, Tanaka et al. 1999). Most growth-rate adjustments

Tab. 3. Elements in the structure of dormancy responses in the life cycle to illustrate the range of possibilities

element	one extreme of the response	the other extreme of the response
default starting-response (in the absence of specific signals to the contrary)	development	delay ("obligate diapause", "parapause")
type of response	single, fixed	continuous, plastic
type of delay	minor slowdown	complete arrest
number of components in a single dormancy	one	many
number of successive inductions possible	one	several ("re-entry")
variability	little variation, normally distributed	wide or programmed variation
sensitivity to environmental cues	none ("obligate", fixed)	continuously responsive
type of control	direct, single factor ("quiescence")	indirect, multiple factors ("diapause" and related responses)
default ending-response	passive ("horotelic")	active ("tachytelic")
number of dormancies in the life cycle	one	multiple or successive dormancies ("programme")
number of alternative routes	none (fixed or simple life-cycle)	many (multiple pathways, complex life cycles)
duration of the life cycle	days	years

fine-tune development to ensure that active or dormant stages coincide with appropriate times of year (see Danks 1987: chap. 10, 1991 for examples), whereas many complete stoppages of development coincide with adverse seasons. A preoccupation with marked developmental arrests therefore tends to undervalue the role of dormancies in the seasonal timing of activity.

Number of components in a single dormancy

A single period of dormancy may include only one component, as in simple temperature-based quiescence, but usually involves a series of stages of diapause from induction to completion. In such instances, responses to environmental conditions or to neuroendocrine agents change throughout the diapause period, showing that the developmental delay is organized into a number of steps. The internal complexity of such dormancies allows for relatively precise control of their onset and completion.

Number of successive inductions possible

In most species, when diapause in a given stage ends, the life cycle proceeds to a subsequent instar without further delay. However, in a few species diapause can be reinduced in the same stage. In most eggs, larvae and pupae this takes place while the insect is still quiescent after a first diapause (e.g., Salt 1947, Church 1955, Friederic 1984, Finch & Collier 1985). In adults, successive diapauses can separate periods of reproduction (Hodek 1971, 1979 and other papers; references cited by Danks 1987: 71). Such reinduction in effect increases the flexibility of the response by allowing a normal, a partial or a delayed end to development or reproduction.

Variability

The pattern of genetic variability in dormancy varies from responses fixed at the same mode in every individual to responses that vary widely in extent or occurrence or are divided into one or more subsets (polymorphism). Most of the latter accord with environments that are unpredictable, where genetically variable responses – unlike the plastic responses already noted – afford insurance against catastrophes that cannot be forecast by available cues. In these unpredictable environments, genetic differences are used to spread risk ("bet hedging") (cf. Danks 1983, 1987; 190–192, Hanski & Stahls 1990, and see below).

Sensitivity to environmental cues

Dormancy in some species appears to be insensitive to conditions. Other species respond continuously to environmental information. This difference parallels differences in the types of response already outlined, but with a focus on the environmental signals rather than on development. Many species strike a balance between the extremes, using both responsive and pre-programmed components (e.g., Dixon & Kundu 1998).

Type of control

Control of dormancy can range from simple direct inhibition of development (quiescence) to the effects of a range of token stimuli on a number of systems. Of course, such effects can be centrally coordinated. Other facets of seasonal adaptation such as cold hardiness, colour change and energy storage are correlated, and can also be coordinated, with life-cycle timing and control.

Default ending-response

In a similar way as for the start of dormancy, either development or dormancy may be the default ending-response, so that dormancy either elapses automatically or it persists unless ended by specific treatments. In other words, development resumes either because diapause ends spontaneously without requiring a change of conditions, or actively because development is stimulated by outside factors. Those alternatives were labelled respectively horotelic and tachytelic responses by Hodek (1981, 1983, see also Hodek & Hodková 1988). Like starting-responses, therefore, ending-responses can be either passive or active. Passive (conservative or fail-safe) modes protect against premature release from dormancy by temporarily favourable environments, whereas active responses can be used to take advantage of environments that might prove more favourable than the norm.

Number of dormancies in the life cycle

In some species, development can vary only during a single stage. The life cycles of many other species include several different stages during which development can be adjusted (e.g., Shindo & Masaki 1995 for early and late larval life), so that several alternative life-cycle routes are allowed depending on circumstances (see below). In eggs of the Mediterranean grasshopper *Eupholidoptera smyrnensis* (Brunner, 1882), up to four successive diapauses and two quiescences may take place during a single egg stage (Ingrisch 1986a, b), leading to widely different periods before hatch.

Number of alternative routes

Many species in sheltered habitats have fixed life cycles that, although they may vary in duration according to temperature, always follow a single, simple route. Complex life cycles (Danks 1991) contain a number of components (see above) and so generate different responses (quiescence, diapause, growth rate) governed by different factors (photoperiod, temperature, water, food) at different stages. More than 18 alternative life-cycle pathways can thereby be generated in some species that have been investigated (e.g., Wardaugh 1986).

Duration of the life cycle

By the same token, the duration of the life cycle, and hence the numbers of seasonal cycles experienced, varies chiefly according to how complex the life-cycle pathways are. For example, dormancy-free, parthenogenetic morphs of some aphids take only a few days per generation in summer. Conversely, successive diapauses extend the larval life of some high-arctic moths for many years (e.g., Kukal 1991, Danks et al. 1994). Here is another contrast between a rapid opportunistic mode of response and a delayed conservative one, reflecting the very different environments of these species.

CONTROL OF DORMANCY RESPONSES

The life-cycle programmes built up from the components just outlined are controlled through a variety of internal and external mechanisms acting in concert. In parallel with the last section, this section does not treat the many individual cues that control dormancies, such as photoperiod and temperature, but rather considers the overall genetic and environmental aspects of the responses. (For a summary of the detailed components see Danks 1987: chaps 6–9.)

The overall aspects are summarized in Tab. 4. Internal factors stem from genetic differences among strains, sexes and individuals, while the ways in which external factors are used depends on their relevance and value for determining seasonal time and its correlates.

Strain differences

Climate and other factors differ geographically. Therefore, most species have locally adapted strains, except for widely dispersing panmictic species. Traits that can be selected for include differences in how growth rates respond to conditions, as well as differences in the existence and incidence of diapause, its sensitive and responsive stages, the cues that are effective, and their uses in induction, diapause intensity and diapause development. Hence local strains may even differ in basic features of the life cycle like voltinism, dormant season, or reproductive season.

Tab. 4. Key elements of the factors controlling dormancy

element	explanation	sample differences or sample factors
internal factors		
strain	geographic differences	many differences in incidence of diapause, voltinism, sensitive or responsive stage, photoperiodic response in induction, diapause intensity, cues for diapause development, etc.
sex	male and female responses differ	male diapause responses often less marked
individual variation	genetic differences among individuals	polymorphisms in seasonal emergence, prolonged diapause, etc.
mechanisms	internal control mechanisms	chiefly neuroendocrine
External factors		
reliability	correlation with seasonal position and predictability of seasonal change	photoperiod and thermoperiod reliable; food often reliable; other factors mostly not reliable
frequency	availability for regular monitoring	temperature, moisture, photoperiod and thermoperiod frequent or continuous; other factors mostly intermittent or variable
recognizability	availability of sensors and seasonal rate of change	most factors easily recognizable by sensors but their rate of change not easily recognized

Some responses, notably to photoperiod, show clear latitudinal patterns, typically clinal but sometimes abrupt. However, many other differences appear to fall into mosaic rather than clinal patterns, reflecting changes from place to place in how various cues, resources and other components interact. The existence of mosaic and even discordant patterns requires that several aspects of dormancy responses be investigated for one species over a wide geographic area. Investigations of development, diapause, food plants, size and other life-cycle features for swallowtail butterflies (Scriber 1994 and references cited there) show how fruitful such a broad approach can be.

Sexual differences

Dormancy is generally more marked in females than in males, as evidenced by a greater tendency in various species for females to sequester food reserves, enter diapause and maintain diapause. In some species, only females survive the adverse season. In addition, in protandrous species the post-diapause developmental period normally is longer in females than in males. Consequently, in many species, especially if the female is large, the life cycle of females is longer than that of males (e.g., Kaplin 1995).

These tendencies have usually been attributed to two main factors. The greater cost of developing and maintaining eggs than sperm means that decisions about egg development often are final. The cost of depositing eggs that either will not survive the adverse season or give rise to larvae that cannot develop in time to survive it punishes late reproduction. Both factors favour entry into diapause especially by females as the season wears on.

Individual variation

Although many dormancy characters show a range of variation typical of biological characteristics, as reflected by the normal distribution, several patterns of genetic difference appear to be specifically programmed as adaptations to seasonal events. Such polymorphisms include groups that emerge at different times within a season, for example in spring and summer (Danks 1987: tab. 26), and groups that remain dormant for different numbers of seasons, thereby prolonging the duration of dormancy for up to 17 years (Powell 1989, Danks 1992). Even the numbers of annual generations and their pattern can be polymorphic and not just plastic (Gilbert & Raworth 1998 for fundatrix polymorphism in an aphid). Although the onset of different durations of prolonged diapause appears to reflect different genetic propensities, in a number of species the delays appear to end partly in response to external cues.

These polymorphic responses are correlated with unpredictable environments (see Variability above). The more delayed sections of the population typically are less common, to an extreme degree in some instances of very prolonged diapause where only a tiny percentage of individuals remains dormant for many years. This pattern would be expected because the likelihood that conditions will be continue to be unsuitable, and hence the need for insurance, becomes smaller over time. At the same time, these very delayed individuals are more costly, because they must devote energy for maintenance (in lieu of future reproduction) and their delayed reproduction also represents lost potential in the rate of increase.

Although some of the polymorphisms are rare, the fact that they occur in many different species means that understanding the internal controls of dormancy may require experiments with larger numbers of individuals and conducted over longer periods than might be anticipated (cf. Danks 1983). In particular, these insurance responses are important even when their incidence is low, because most insect populations recover rapidly from small numbers of survivors after misfortunes ranging from pesticide treatments to climatic catastrophes. Consequently, experimental variations in dormancy should be examined explicitly for potentially adaptive polymorphisms, and not just viewed as "experimental noise".

Internal control mechanisms

Internal mechanisms to control dormancy are implemented chiefly at the neuroendocrine level. They will not be considered here except to note that they are the key link by which responses to external factors are integrated into the internal milieu.

External control

External control is effective when particular environmental factors are both visible and informative, especially on a seasonal basis, as to the current or future suitability of habitats for development or reproduction. The second part of Tab. 4 lists features of some potential cues (for further discussion, see Danks 1987: chap. 6). Which cues are likely to be effective (and therefore which ones should be included or monitored for experimental work) also depends on the particular habits and life cycle of the insect. For example, inside opaque habitats photoperiodic cues are difficult to detect even though response thresholds can be very low; in habitats buffered against daily changes, temperature cues provide more reliable information compared to the noisy signals experienced elsewhere.

Note that the reliability of cues stems chiefly from their precision in indicating seasonal time, which in a given place normally correlates closely with climatic and other ultimate factors. The ultimate factors themselves are less often directly signalled.

CONCLUSIONS

Many strands of adaptation are woven into dormancy responses, especially where natural environments are seasonal. This synopsis confirms the view that a given dormancy can be understood only *in the context of the life cycle viewed as a whole, together with the relevant environment* viewed as a whole. Dormancies have multiple purposes, they are assembled from multiple components with a range of levels of expression, and they are controlled through multiple internal and external factors. Moreover, the same requirements can be met by different responses or sets of responses (e.g., either obligate diapause or wide variability could be part of a response to unpredictable environments); and the most reliable environmental signals usually are not the same as the ultimate selective factors.

Therefore, in my view dormancies are best studied from many aspects simultaneously, based on the widest possible appreciation of their place in the complete life cycle of any particular species. Such an approach will require more thoughtful experimentation, measurement, reporting and analysis than still is customary in much of the work on dormancy and development in insects (compare Danks 2000), as well as an effort to dispel the outmoded idea that dormancy operates only as a simple developmental switch.

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I am especially happy to contribute a paper on the nature of dormancy to this issue in recognition of Professor Ivo Hodek, because Prof. Hodek has correctly promoted in several ways the idea that diapause is a dynamic state and not the sort of static condition once assumed.

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BOOK REVIEW

PETRY F. (volume editor): **Cryptosporidiosis and Microsporidiosis.** Contributions to Microbiology. Vol. 6. (series editor: A. Schmidt). Basel, S. Karger Medical and Scientific Publishers, 2000. XII+268 pages. Format 168×240 mm. Hard cover. Price CHF 218.–, USD 189.75. ISBN 3-8055-7050-3

As stated in the note of the series editor, cryptosporidia and microsporidia are relevant parasites that are mainly responsible for intestinal disturbances in humans. These protozoa are generally not well understood yet and they remain enigmatic for clinical microbiologists. Research in this field makes fast progress, with a lot of new knowledge steadily arising. As accentuated in the preface by F. Petry (Mainz), cryptosporidia and microsporidia are protozoan parasites that have emerged as human pathogens over the last two decades. Although they belong to quite different taxa, both groups of parasites have many features in common: they have been known as parasites of animals long before cases of human disease have been described. With the emergence of the acquired immunodeficiency syndrome, they have been recognized as important opportunistic pathogens of patients with an impaired defence system. In both groups of pathogens, the transmission pathways are not fully understood. The progress that has been achieved in the cell biology and molecular biology, the immunology and other aspects of the parasites has been enormous and is reflected by hundreds of scientific publications each year. The volume is composed of two parts.

The part on **cryptosporidiosis** is arranged in 6 chapters written by 14 authors from USA, Great Britain and Germany. The chapter on biology and the nature of *Cryptosporidium* centres attention upon natural history and taxonomy including species designation, genotypic and phenotypic variation, life cycle and intracellular development. *In subsequent chapters discussed are clinical aspects of cryptosporidiosis, laboratory diagnosis of C. parvum,* host immune responses, notably T-cell-dependent responses to infection, T-cell mediated immunity and production of interferon gamma, involvement of cytokines in immunity, antibodies and cellular responses at the cellular level. Chapter on gene discovery in *C. parvum* provides insights into the molecular karyotype, expressed sequence tags of sporozoites, genome survey sequences, protein motifs in unidentified sequence tags and the construction of a physical map of the *C. parvum* genome. Concluding chapter is dedicated to the epidemiology of cryptosporidiosis, nominally to the species in the genus *Cryptosporidium*, variation within *C. parvum*, DNA detection, and environmental detection.

Subsequent part on **microsporidiosis** presents a collection of 5 chapters compiled by 7 authors from USA, *France and Switzerland. The chapter on biology of microsporidia is devoted to the natural history and characters* of the group and to the taxonomy, in particular to the cell organization, classification and to microsporidians occuring in humans. Interestingly, suggested is the phyletic relationship between microsporidia and fungi: sharing common gene sequences for β-tubulin, the presence of chitin and trehalose in the spore, the occurence of diplokaryotic stages and the intranuclear mitotic spindle. In subsequent chapters are delineated diagnosis and clinical aspects of human microsporidiosis and immunology of microsporidiosis. Chapter dealing with molecular phylogeny and diagnostic approaches of microsporidia accentuates additional evidence for the view that microsporidia may be related to the fungi. Concluding chapter gives an account of epidemiology and zoonotic aspects of microsporidia in mammals and birds.

Each chapter is provided with a comprehensive list of references exceeding mostly 100 citations. The textual part is illuminated by 28 figures, 9 in color, composed of line drawings, light and electron microphotographs featuring parasites and their life cycles, pathways for energy metabolism, diverse diagrams, a dendrogram of microsporidian phylogeny, histopathological abnormalities, endoscopic and radiological findings. Moreover, there are 19 tables offering overviews of taxonomic and differential diagnostic features, detection and identification, host and environmental risk factors, hosts and geographical distributions, prevalence rates, and clinical patterns. This volume provides most complete and balanced coverage of essential aspects of the pathogens as well as the diagnosis and clinical correlations of the disease they cause. It is set to become a valuable reference for parasitologists, protozoologists, molecular biologists, clinical microbiologists, epidemiologists and specialists in infectious diseases.

Jindřich Jíra

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Adult diapause of a monovoltine water strider, *Gerris gracilicornis* (Heteroptera: Gerromorpha)

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Abstract. Overwintered adults of a water strider, *Gerris gracilicornis* Horvath, appeared on a pond during the middle of March to the beginning of April in Kochi (33.3 °N), Japan. Nymphs of the first generation developed in May and June, and adults emerged in the last half of June. The first-generation adults disappeared from the pond without reproducing in July. All adults that develped and were kept in nymphal and adult stages under 15.5L–8.5D, 20 °C, 15.5L–8.5D, 30 °C, or 18L–6D, 20 °C entered reproductive diapause. Longevity of adults reared and kept at 30 °C was 50 days on average and much shorter than 164 days at 20 °C. On the 40th day after adult emergence, some of adults were transferred to 9.5L–14.5D, 20 °C, and the others were kept under 15.5L–8.5D, 20 °C. Most surviving adults were chilled at 7 °C for 30 days from the 180th day after emergence. On the 210th or 220th day, all the adults were moved to 15.5L–8.5D and 20 °C, which represents spring conditions. When they were reared and kept under 15.5L–8.5D, most adults that experienced short days of 9.5L–14.5D followed by chilling, ended their diapause and began to lay eggs within 30 days under the spring conditions. Only short-days or only chilling induced 20 or 40% of the adults to end diapause, respectively. When they were reared and kept under 18L–6D, more than 80 % of the adults that experienced chilling at 7 °C ended diapause. In Kochi, both short-days in fall and the following chilling in winter seem to be needed to end such a long diapause, persisting for more than 7 months even in Kochi, which is located in a critical region between subtropical and temperate zones.

Obligatory diapause, diapause development, short-days during winter, chilling, monovoltinism, Heteroptera, *Gerris gracilicornis*

INTRODUCTION

Insect diapause was defined by Henneguy (1904) as "the arrest in ontogenetic development" at a specific stage during life history. Diapause consists of three stages of "diapause induction", "diapause development" and "end of diapause development" (Danks 1987). Moreover, diapause can be separated into "facultative diapause" in which induction was determined by environmental conditions, and "obligatory diapause" which is induced automatically at a specific stage (Tauber et al. 1986). Diapause development can also be controlled by such environmental conditions as photoperiod and temperature (Danks 1987), or can go on according to passing time (Hodek 2000).

Water striders in the subfamily Gerrinae overwinter as adults (Spence and Andersen 1994), and gerrids species show mono-, di- or trivoltinism in the temperate zone (Andersen 1993, 2000, Harada et al, 2000). Monovoltine species (*Gerris lateralis* Schumm., *G. costae* (H.-Sch.) and *G. gibbifer* Schumm.: Kopfli et al., 1987; *G. pingreensis* Dr. et Hot.: Spence, 1989) in temperate zone might show obligatory diapause. *G. gracilicornis* Horv. can be observed on water surfaces only during a very short period from April to July in the plain area in Kochi and might show obligatory diapause even in Kochi, which is located in the critical area between temperate and subtropical zones.

This study aims, first, at clarifying whether *G. gracilicornis* shows monovoltinism in Kochi; second, whether adult diapause is obligatory or not; and, third, how photoperiods and chilling during diapause development affect diapause development and its completion.

MATERIALS AND METHODS

Sampling

Timed-catch sampling of adults was done on the water surface near the shore of a small pond (174.5 m^2) located in the campus of Kochi University in Kochi (33 °N), Japan for 30 min. every 7–10 days during April to August, 1995 with a round net of 30 cm in diameter. Nymphs were sampled from a water-surface area of about 8 m^2 by sweeping another net (45 cm in diameter). Overwintered adults were collected in April, 1995 from a storage pond for agriculture on the foot of a hill in Kochi (33 °N) where water temperature was less than 23 °C even in mid-summer. The overwintered females and the eggs they laid were kept under 15.5L–8.5D, at 20±2 °C and recently hatched 1st instars were used for the experiment.

Is adult diapause of Gerris gracilicornis obligatory ?

Gerris gracilicornis is monovoltine in Kochi (Harada, unpublished) . This species distributes very widely in the latitudal axis from 20° to 60° N from eastern to east-southern Asia (Andersen & Chen 1993). Moreover, populations can be seen only in water bodies where the water temperatures is less than 23 °C even in mid-summer in Kochi. In more northern area where air temperatures are less than 23 °C through the year, this species might show a bivoltine life cycle.

(1) In that case, extremely long photoperiods (which this species does not experience in Kochi) might induce direct breeding.

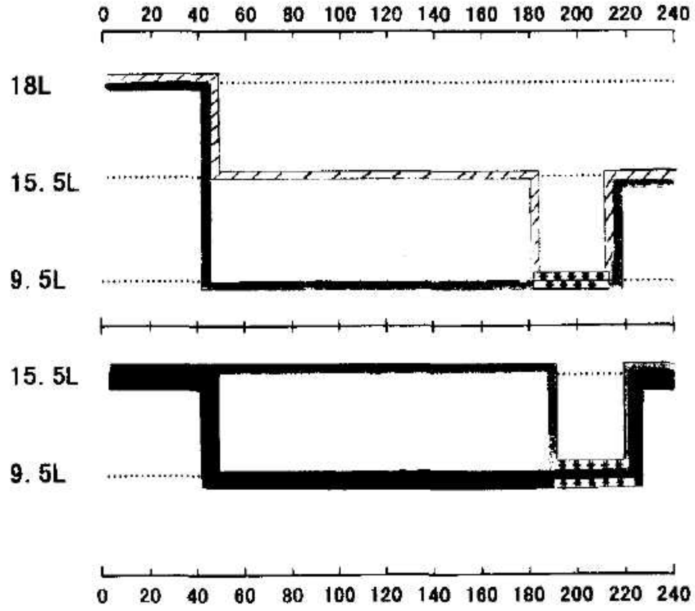

Fig. 1. Schematic presentation of experimental schedules 18L, 15.5L and 9.5L show 18h light – 6h dark, 15.5h light – 8.5h dark and 9.5h light – 14.5 h dark, respectively.

(2) High temperatures in summer may also induce direct breeding.

To test the 2 hypotheses, 1st instars just after hatching were reared under long-days of 18L–6D or at 30 °C and it was determined whether or not these conditions can prevent adults entering diapause.

Factors that can end adult diapause

Figure 1 shows the experimental schedules used to examine what factor(s) which is (are) effective to end adult diapause. On the 40th day after adult emergence, some adults kept under 15.5L–8.5D or 18L–6D were transferred to a short day of 9.5L–14.5D. The remainders were kept under 15.5L–8.5D. On the 180th or 185th day, they were moved from 20 °C to 7 °C and kept there for 30 days under 9.5L–14.5D. Then they were transferred to 15.5L–8.5D and 20 °C, which are similar to spring conditions. The number of eggs deposited was counted every day.

RESULTS

Sampling

Overwintered adults of *Gerris gracilicornis* appeared on water bodies on (or before) 7th to 15th April, 2000 (Fig. 2). The number of overwintered adults caught gradually decreased from the beginning of May until June. First instars of the next generation appeared in the middle of May. They developed in May and June and adults emerged in June. The number of adults caught decreased gradually in July and none could be seen at the beginning of August.

Nymphal development

When individuals developed at 20±2 °C, the nymphal period was 31–33 days (33.5±1.9 days=Mean±SD under 18L–6D, 30.6±SD under 15.5L–8.5D), whereas it was 20±1.7 days at 30±2 °C

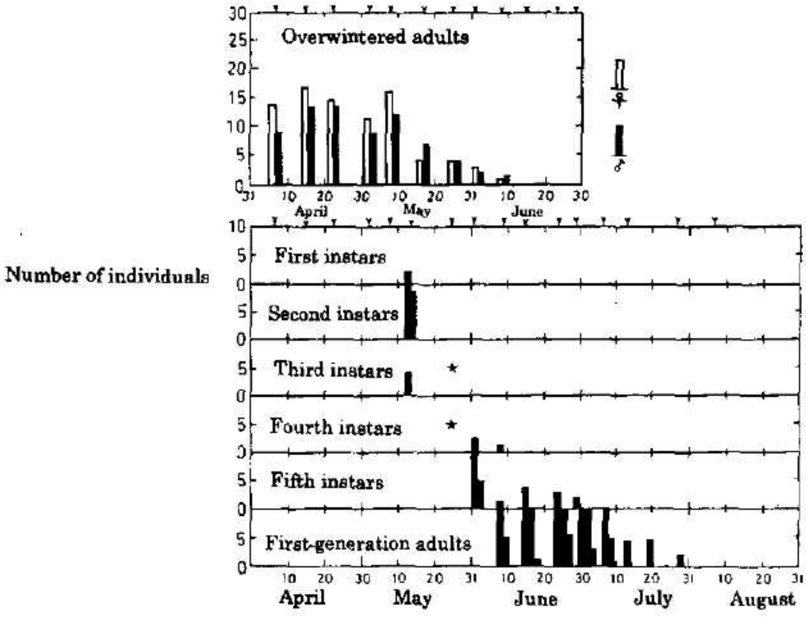

Fig. 2. Seasonal changes in the individuals of the water strider *Gerris gracilicornis* as shown by timed-catch sampling.

under 15.5L–8.5D. 90.8% of newly hatched nymphs (n=185) survived until adult emergence, when they were reared at 20±2 °C and under 15.5L–8.5D. The survival when reared under 18L–6D and at 20±2 °C was 49.8% (n= 203) and significantly higher than 40.1% (n=207) under 15.5L–8.5D at 30±2 °C (χ^2-test: Person's $\chi^2_{cal.}=3.864, p=0.049$).

Is adult diapause of Gerris gracilicornis obligatory ?

All the adults in the three environmental conditions laid no eggs for the first 40 imaginal days. Twelwe pairs of adults in each of the three conditions were dissected on the 40th day after emergence. No females had mature oocytes and the volume of testes was very small (less than 1/5 of that in reproductive adults) in all the adults [15.5L–8.5D, 20 °C: 98.7±14.5 ($\times 10^{-4} mm^3$); 15.5L–8.5D, 30 °C: 126.8±28.9; 18L–6D, 20 °C: 103.9±18.8]. All adults had well developed flight muscles. These results suggest that *G. gracilicornis* enters obligatory diapause.

Survival on the day of transfer to spring condition

When the adults experienced both short-days and chilling, the percent survival was 39% of newly emerged adults (n=46) and it was significantly higher than 23% of emerged adults which experienced only short-days (n=150; χ^2- test,$\chi^2_{cal.}= 4.514, p=0.034$). Adults reared under 18L showed significantly higher survival (67%) than adults reared which under 15.5L (40%)(χ^2- test when they were kept under 15.5L,$\chi^2_{cal.}=6.722, p=0.010$; when they were kept under 9.5L,$\chi^2_{cal.}=6.299, p=0.012$).

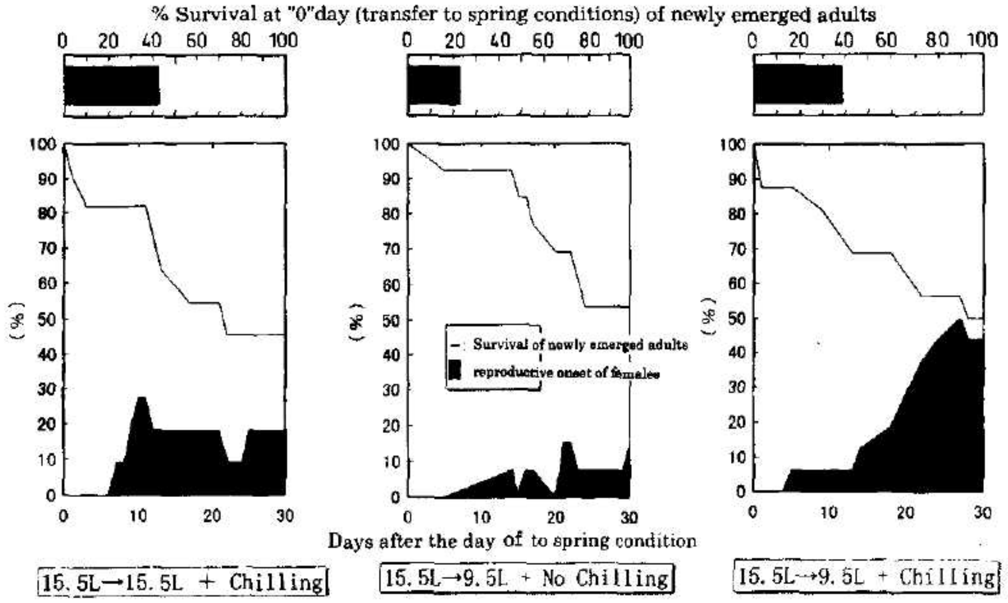

Fig. 3. Effects of short-days and chilling during diapause development on survival and reproductive onset of females when they were reared under 15.5L–8.5D. 0 day in figure corresponds to 180–190 days after adult emergence.

Factors that can end adult diapause

Eighty six percent of adults that experienced both short-days and chilling laid eggs before the 30th day after transferring to spring conditions, when they had been reared under 15.5L–8.5D (Fig. 3). When they experienced only short-days or only chilling, only 30 or 40% laid eggs, significantly less than the 86 % (Fisher's exact probability test: p=0.014). 80 % of adults reared under 18L–6D laid eggs within 30 days after transferring to spring conditions, whereas when they had been under 15.5L–8.5D throughout the rearing period the percentage was 40 (Fisher's exact probability test: p=0.045 when they experienced not short-days but chilling) (Figs 3, 4).

When they were reared under 18L–6D, the preoviposition period after the transfer to the spring conditions tended to be shorter than that when reared under 15.5L–8.5D (One way ANOVA: F=3.984, p=0.052).

When they were reared under 15.5L–8.5D, fecundity (Mean±SD=73.4±69.0, n=7) of the adults that experienced short-days before chilling was significantly more than that (9.8±13.4, n=4) of adults that did not experienced (Mann Whitney U-test: z=–1.989, p=0.047). The adults (53.9±51.9, n=14) reared under 18L–6D were significantly more fecund than those (9.8±13.4, n=4) reared under 15.5L–8.5D (Mann Whitney U-test: z=–2.128, p=0.033).

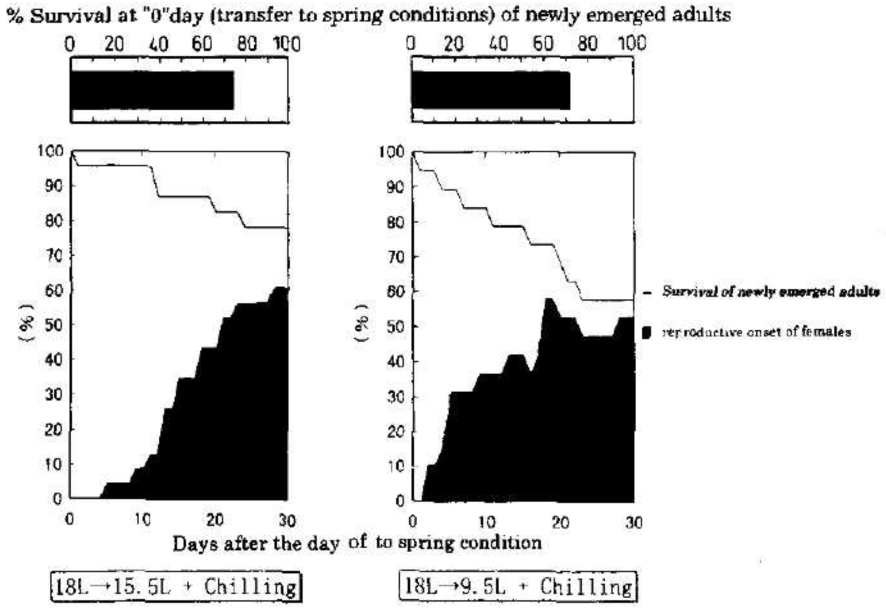

Fig. 4. Effects of short-days during diapause development on survival and reproductive onset of females when they were kept under 18L–6D.

DISCUSSION

Diapause induction of *Gerris gracilicornis*

Gerris gracilicornis is monovoltine in Kochi, and diapause adults disapper in July from a pond in Kochi plain (Fig. 1). However, according to rearing experiments under natural conditions (Harada, unpublished), most of the adults in reproductive diapause can be seen on the water surface of an experimental aquarium (half water and half land) at the end of September. Overwintering adults moved from water surface to land in October and the beginning of November. They hid themselves under the fallen leaves and adopted diapause posture at the beginning of November. They are in reproductive diapause for very long period from July to the next March. However, a corresponding reduction of activity is delayed by three months. Such delay is unusual for Gerrinae bugs: timing of entering reproductive dipause is corresponding with that of moving from water to land (diapause place) followed soon by reduction of activity (Spence & Andersen 1994, Harada et al. 2000). In August and September, they are very actively striding on water surfaces in natural conditions and sometimes flight behaviors can be observed. One speculation is that they leave water surfaces in the plain at the beginning of July and migrate to water bodies elsewhere, eg. lentic water in hills or mountains, because water surface there would be less than 22 or 23 °C. Such behaviour would avoid high temperatures in the plain area during summer. At 30 °C, only 40% of newly hatched 1st instars can survive at emergence, whereas it was 90% at 20 °C. Such a physiological limitation on heat hardiness might force them to maintain high activity in striding and flight even through they have already entered reproductive diapause.

Obligatory diapause

Both extremely long-days (18L–6D) and high-temperature of 30 °C cannot prevent reproductive diapause. Individuals may enter reproductive diapause automatically regardless of environmental conditions during the nymphal period. However, 18L–6D can accelerate diapause development, or the diapause itself is not so deep: when they are reared under 18L–6D diapause may end earlier than when reared under 15.5L–8.5D (Figs. 3,4). At higher geographic latitudes, the temperature in summer is not so high. *Gerris gracilicornis* might develop a bivoltine life cycle in more northerly populations. Even in the Kochi strain, diapause can easily be completed when they are reared under very long photoperiod of 18L–6D. This response means that they can measure photoperiodic information even in the nymphal period and pass it on to control diapause.

Factors that accelerate diapause development of adults

In Kochi, both short-days in fall and the following chilling in winter are needed for accelerated diapause development and subsequent termination of reproductive diapause. The requirement for both factors to terminate diapause can be linked to the fact that if only chilling were needed to end diapause, diapause might end in the unsuitable season of mid winter, because of unpredictable low temperatures. Kochi is located at the critical region between subtropical and temperate areas. A monovoltine life history is unique in such a warm region. However, having only one reproduction per year is potentially risky for maintaining the population. Nevertheless, a high percentage (about 91%) of newly hatched nymphs can be grown up safely if food is sufficient, and the cuticle of the body wall is very thick and hard, so that high drought hardiness is very likely. The two factors could compensate for the risk of only one chance to reproduce per year. As a result, nymphal habitats in July and August will be passed in the more resistant adult stage like as in some noctuid moths, tropical butterflies, coccinellids, flies, and limnephilid caddisflies (Danks 1994).

Danks (1987) reviews the role of low temperature (as in winter under natural conditions) as a cue for diapause development in a very large number of insects from temperate regions. For example, chilling is needed for the completion of diapause in many insects like a lepidopteran *Lymantria* *dispar japonica* (Masaki 1956), and a coleopteran *Atrachya menetriesi* (Ando 1983). Hodek & Hodková (1988) and Hodek (2000) claimed that low temperature in winter is not necessary for some insects to go on to diapause development but rather it goes on automatically according to passing time. However, *Gerris gracilicornis* in Kochi needs low temperature in winter for the end of adult diapause in the next spring.

Two-step responses are shown by some insects (e. g. a coleopteran *Pterostichus nigrita*: Ferenz 1977): short days followed by long days are needed for reproductive maturation in the ovaries. Short days promote previtellogenesis and then the long days induce vitellogenesis (Zaslavsky 1972, Nijhout 1994). *G. gracillicornis* may be added to the group in which two-step responses can be seen.

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BOOK REVIEW

GILLES H. M. (editor): **Protozoal Diseases**. London, Arnold, a member of the Hodder Headline Group, 1999. Co-published in the United States of America by Oxford University Press, New York. X+707 pages. Format 198×270 mm. Hard cover. Price Lstg 145.00. ISBN 0-340-74090-6

The editor is an acknowledged specialist, emeritus professor of tropical medicine affiliated with the School of Tropical Medicine at Liverpool. The list of contributors comprises 52 international experts from around the world: Europe, USA, Africa, Asia and Latin America. It is mentioned in the preface, that this book has had an unusually long gestation period. The volume is composed of 19 chapters. Each chapter presents an overview of a disease caused by protozoan parasites. Individual chapters dealing with most important protozoal diseases are constructed by a general framework enclosing historical perspectives, biological characteristics of the parasite and host-parasite relationships, pathological aspects, clinical manifestations and differential diagnosis, laboratory diagnosis and immunological tests, treatment and management, epidemiology and control, and are concluded with a list of references. Chapters describing arthropod-borne protozoal diseases focus also on biological characteristics and epidemiological importance of ectoparasitic vectors = blood-sucking insects: anopheline mosquitoes, tse tse flies (genus *Glossina*), triatomine bugs and phlebotomine sandflies.

Chapter 1 offers an exhaustive treatise of malaria. Embracing 235 pages it presents the most extensive part of this book – 33 per cent of the page extents. It is compiled by 10 authors altogether. The list of references includes a respectable number of citations – 1375 items.

Chapter 2 is concerned with babesiosis discussing *Babesia* species capable to infect humans and cause a serious illness. Chapters 3 and 4 examine causes of human morbidity and mortality due to African and American trypanosomes: sleeping sickness and the Chagas disease. Chapter 5 centres attention on toxoplasmosis. Chapter 6 constitutes a highlight of leishmaniases – this comprehensive chapter is compiled by 11 authors – it embraces 117 pages and 806 citations. Discussed are 20 *Leishmania* species, causative agents of the Old and New World visceral and cutaneous leishmaniases, and diverse clinical features of the New World mucocutaneous leishmaniasis.

Chapters 7 through 12 are dedicated to intestinal parasites and infections: amoebiasis, *Dientamoeba fragilis*, giardiasis, balantidiasis, and cryptosporidiosis. In chapter 13 on *Pneumocystis carinii* is discussed the taxonomic position of this organism – ultrastructural and molecular biological studies have placed it most firmly into the fungal kingdom. Chapters 14 through 19 provide a look at sarcosporidiosis, microsporidiosis, isosporiasis, *Chilomastix mesnili*, potentially pathogenic free-living amoebae, and trichomoniasis.

The volume is extensively illustrated by schematic line drawings and black-and-white photographs: life and transmission cycles of protozoan parasites, pictorial presentations of laboratory procedures and techniques for the diagnosis, diverse diagrams, light and electron microphotographs, charts of global distribution of protozoan infections, views of terrestrial biomes, pathologigal and histopathological abnormalities, photographs illuminating clinical conditions, skin lesions and ophthalmological findings, radiographs, and others. In addition, there are numerous summary-type tables overviewing taxonomical classification schemes, prevalence data and worldwide distribution of protozoal infections, principal nosodemiological features, classification of antiprotozoic drugs, therapeutic and chemoprophylactic schedules.

This publication presents a most comprehensive up-to-date handbook of clinical protozoology comparable only with the "Parasitology" of F. E. G. Cox et al. (1998 – for review see Acta. Soc. Zool. Bohem. 62, 226, 1998). Incorporated are all pieces of recent knowledge on protozoal diseases. Four of the chapters on major diseases, that is malaria, leishmaniases, African trypanosomiases and Chagas disease, present as such mini monographs written by foremost authorities in the field. Most chapters reflect recent information on emerging protozoal diseases, notably those in connection with immune disorders. Analyzed are contemporary epidemiological situations, new discoveries in the field of molecular parasitology and genetics, genome structures, modern diagnostic procedures such as DNA probes, antigenic structure and diversity, immunity and disease pathophysiology, and more. There is presented an extensive thesaurus of protozoological bibliography. The readers may only regret the absence of some colour illustrations.

Jindřich Jíra

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Development of *Coreus marginatus* (Heteroptera: Coreidae) fed on seeds of *Rumex obtusifolius*

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Abstract. The length of the egg and larval development of *Coreus marginatus* (Linnaeus, 1758) was investigated at constant temperatures of 19.2 °C, 21.0 °C, 25.0 °C and 27.8 °C. For egg development, the lower developmental threshold (LDT) temperature was estimated to be 12.9 °C and sum of effective temperatures (SET) 142.9 day degrees (dd). The larvae were fed seeds of *Rumex obtusifolius* L. The mortality increased with decreasing temperature. Using data for the first three larval instars, where mortality was low, LDT was calculated to be 13.9 °C. No larvae completed development at 19.2 °C and few at 21.0 °C and 25.0 °C. At 27.8 °C 75 % of the larvae completed their larval development. Using the data on developmental length at this temperature the SET for larval development was estimated to be 556 dd and SET for complete pre-imaginal development (egg + larva) 742 dd. The long developmental time and high larval mortality indicated that a diet consisting only of *R. obtusifolius* seeds was unsuitable for the development of *Coreus marginatus*.

Temperature, development, egg, larva, *Coreus*, Heteroptera, *Rumex*, seed

INTRODUCTION

The rate of pre-imaginal development in ectotherms depends on temperature in a deterministic manner. The duration of total development or that of particular stages decreases with increase in ambient temperature. Consequently, the development rate which is a reciprocal of development time increases directly proportionately with temperature. At the range of ecologically relevant temperatures the rate/temperature relationship is linear but becomes non-linear at the high temperatures and, in some species, also at low temperatures (e.g. Hodek 1958). Several studies attempted to describe the effect of temperature on development rate by a non-linear relationship which could be applied to data recorded over the whole range of tolerated temperatures (e.g. Wagner et al. 1984, Lactin et al. 1995, Briere et al. 1999). However, limiting the analysis to the range of temperatures where the relationship is linear has several advantages (Ikemoto & Takai 2000). Projecting the linear regression enables the calculation of important characteristics of the development/ temperature relationship: the lower development threshold (LDT) and the sum of effective temperatures (SET). These thermal constants of development enable the development times over a range of ecologically relevant environmental conditions to be predicted and facilitate comparisons between species (Honěk 1996a). Many studies confirmed this relationship for insects and related arthropods (Honěk & Kocourek 1990, Honěk 1996b, Kiritani 1997). While thermal constants for non-growing development stages, like eggs and pupae, are typical for particular populations the SET for larval development varies with trophic and environmental conditions. The variation in the thermal constants between species and between developmental stages within species may be adap-

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Tab. 1 The length of development (D), development rate ×100 (r), number of individuals that completed the development (n) in eggs and L1 to L5 larvae of *Coreus marginatus* at four experimental temperatures (T, °C).

T		eggs	L1	L2	L3	L4	L5
19.2	D	21.50±1.66	8.04 ± 2.25	12.08 ± 2.74	14.28 ±1.14	13.83	–
	r	4.65±0.36	13.39±3.80	8.78±2.36	7.04±0.54	7.23	–
	n	51	29	15	12	1	0
21.0	D	17.18±1.10	4.67 ± 1.10	10.15 ± 2.73	12.18± 3.06	10.44±3.00	9.67±3.46
	r	5.82±0.36	22.69±5.97	10.65±0.33	8.69±2.10	10.57±3.55	23.35±13.01
	n	24	20	18	14	7	2
25.0	D	10.85±0.63	3.63 ± 0.67	5.69 ± 0.77	5.53 ±0.80	10.05±3.01	14.44±3.34
	r	9.22±0.53	28.58±5.81	17.86±2.28	18.42±2.53	10.70±2.62	7.26±1.44
	n	64	15	15	15	12	3
27.8	D	9.71±0.56	3.76 ± 1.04	4.41 ± 2.10	5.25 ± 0.94	9.09±2.17	17.51±4.34
	r	10.30±0.64	29.00±7.98	32.39±24.73	19.62±3.36	11.59±2.52	6.06±1.46
	n	79	32	32	32	32	24

tive (Gilbert & Raworth 1996). Recently it was argued that LDT may be constrained for groups of species (Dixon et al. 1997). The same is true for LDT of particular developmental stages of a species. This implies constant proportions between developmental stages at different temperatures, a phenomenon named "rate isomorphy" (Jarošík et al. in litt.).

Compared to other insect orders the study of thermal constants in Heteroptera has attracted less attention than would be expected. A literature review provided data for 60 species (Honěk & Kocourek 1990, Honěk 1996b), mainly agricultural pests or predators of agricultural pests. Moreover, many of these populations originated from tropical and subtropical regions. The information on phytophagous species living on wild plants native to cold temperate regions is still fragmentary. A convenient subject for thermal studies is *Coreus marginatus* (Linnaeus, 1758), a natural enemy of several weed species. This coreid species occur in the west-palearctic region (Putshkov 1962). In the Czech Republic the species has one generation per year. The overwintered adults lay eggs in late May – June and the larvae develop through the late spring and summer, until September. While the adults are more polyphagous, the larvae prefer to feed on *Polygonum* spp. and *Rumex* spp. but accept also other broadleaved herbs including *Arctium* spp., *Carduus* spp., *Cirsium* spp., *Onopordum* spp., *Sonchus* spp., *Verbascum* spp. etc. (Putshkov 1962). On *Rumex* spp. the larvae feed on the green parts and on seeds persisting on dry standing shoots from the previous year as well as those maturing in the same year. Since the seeds are available over the whole period of larval development they are probably a convenient source of nutrition. Feeding by *C. marginatus* larvae may be an importnat factor limiting seed production development in *Rumex* spp.

This study reports laboratory experiments aimed at testing the suitability of *R. obtusifolius* seeds for larval development at four constant temperatures between 19.2 °C and 27.8 °C. The experiments provided data for calculating the thermal constants of *C. marginatus* development and also tested whether this species could complete its development on a diet of *R. obtusifolius* seeds.

MATERIAL AND METHODS

Experimental animals

The adults of *Coreus marginatus* were collected in mid-May 2000, on a mixed *Rumex obtusifolius* and *Rumex crispus* L. stand at Praha Ruzyně (50°05'N, 14°16'E, 340 m a.s.l. altitude). The adults were kept in a laboratory at 25–27 °C and natural photoperiod in plastic cups (bottom diam. 6 cm, height 8 cm) covered with nylon fabric. The bugs were supplied with an excess *R. obtusifolius* seeds and a piece of moist cotton. A piece of folded filter paper enabled vertical movement. Immediately after capture the females started to oviposit. Eggs were laid in small groups of 2–15, on the nylon fabric and filter paper, sometimes also on the walls of the plastic cups.

Development

Cohorts of eggs, deposited within 4 h of the start of an experiment, were used. Groups of 5–10 eggs were put into glass tubes (length 5.5 cm, diameter 1.5 cm) closed with a piece of cotton and placed in rearing boxes at different temperatures. Hatching of eggs was monitored 3 times a day, usually at 07:00, 14:00 and 21:00 h. Some freshly hatched larvae were used for experiments on larval development. One freshly hatched larva was placed in each plastic cup. The size of cups and food supplied were the same as used for adults. The moulting of larvae was then observed at 12 h (at 07:00 and 21:00) or (on weekends) 24 h intervals (at 18:00). Moulting was recorded and exuviae removed. The *Rumex* seeds were replaced at ca.10 d intervals. The experiment continued until adult emergence or the death of the larva. The larval instars are indicated as L1, L2, L3, L4 and L5.

Temperature regimes

The experiments were done in climatised boxes, where the temperatures were set at a constant 19 °C, 22.0 °C, 25.0 °C and 28 °C. The temperature where the cups were, and its fluctuations, were measured hourly and average adjusted temperatures for egg and larval development were calculated. The adjusted temperatures T were 19.2 °C, 21.0 °C, 25.0 °C and 27.8 °C. These temperatures were used for calculating thermal constants.

Data processing

The duration of development D at each stage or instar was transformed to its reciprocal, developmental rate R=1/D. The regression of developmental rate R on developmental temperature T was then calculated as R=aT+b, where a and b are constants. Lower developmental threshold was calculated as LDT =–b/a and sum of effective temperatures as SET=1/a. The thermal constants LDT and SET were calculated for eggs and L1, L2 and L3 larvae. Common $\mathrm{LDT}_{\mathrm{L1\ L3}}$ for development of L1 to L3 larvae, and common $\mathrm{LDT}_{\mathrm{E\ L3}}$ for development from egg to L3 larvae were also calculated. The SET for eggs, L1, L2 and L3 larvae were calculated from experimental data. SET for each of the larval instars and total larval development was also calculated using data on developmental length at 27.8 °C and $\mathrm{LDT}_{\mathrm{L1\ L3}}$ as $\mathrm{SET}_{\mathrm{EST}}=\mathrm{D}/(27.8-\mathrm{LDT}_{\mathrm{L1\ L3}})$. The SET for total pre-imaginal development was calculated in the same way using $\mathrm{LDT}_{\mathrm{E\ L3}}$. We also recalculated the data on development of L1, L2 and L3 larvae assuming "rate isomorphy" (Jarošik et al. in litt.). For pre-adult development, the "rate isomorphy" principle assumes the existence of a common LDT determined by a physiological constraint and implies that the propor-

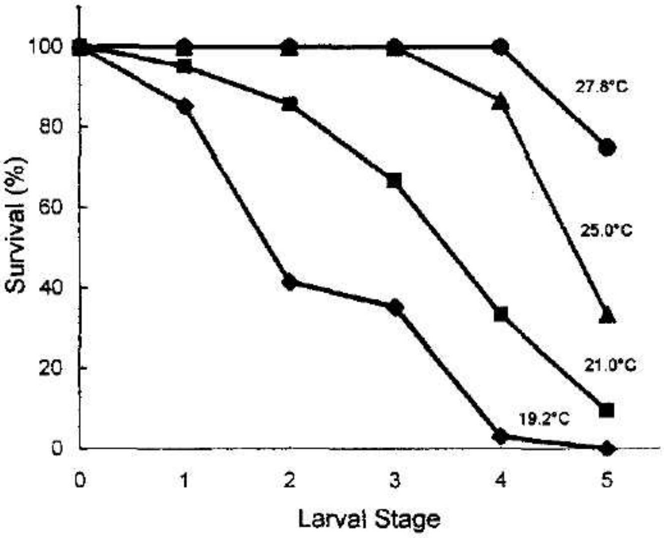

Fig. 1. Larval survival of *Coreus marginatus* at different temperatures – percentage of the initial number of individuals surviving to the end of a particular larval instar and moulting to the next instar or adult.

Tab. 2. The constants of the regression of development rate on temperature (rate = a*temperature + b), lower development threshold (LDT, °C) and sum of effective temperatures (SET, dd) calculated using regression parameters, *estimated sum of effective temperatures (SET_{EST}) for development of 1st to 5th larval instars (L1 to L5),* total larval development (L1–5) and total development (TOT) of the *Coreus marginatus*. The data for larval development were calculated using development length at 27.8 °C and LDT_{L1-L3}=13.9 °C or LDT_{E-L3} = 13.1 °C (see Material and Methods).

Stage	a	b	LDT	SET	SET_{EST}
E	0.0700	0.0906	12.9	142.9	–
L1	0.0175	0.1774	10.1	57.1	52
L2	0.0273	0.4679	17.1	36.6	61
L3	0.0166	0.2549	15.4	60.2	73
L4	–	–	(13.9)	–	127
L5	–	–	(13.9)	–	243
L1–5	–	–	(13.9)	–	556
TOT	–	–	(13.1)	–	742

tions of development spent in particular stages or instars are constant at different temperatures. The proportion of L1–L3 development spent in each instar under different temperatures were calculated, mean proportions for particular instars were determined and the L1 to L3 development times at each temperature were divided by the mean proportions. The recalculated development times were then used for determining adjusted LDT and SET of particular instars.

RESULTS

The course of pre-imaginal development varied with temperature. Mortality in the egg stage was not determined since we could not distinguish between natural mortality and damage caused when detaching eggs from the substrate. The combined mortality was <10 percent at all temperatures. In the larval stage mortality was high and varied with instar and temperature (Fig. 1). Seventy five percent of the larvae completed development at 27.8 °C while all larvae died at 19.2 °C. At 25.0 °C and 21.0 °C the proportion of larvae that survived to the adults stage was 33 % and 10 %, respectively.

The length of pre-imaginal development decreased and its rate increased with increasing experimental temperature (Tab. 1). The temperature requirements for eggs was determined as LDT=12.9 °C and SET=142.9 dd (Tab. 2).

Estimation of the thermal requirements for larval development was negatively influenced by mortality. The high mortality of L4 and L5 larvae at 19.2 °C, 21.0 °C and 25.0 °C caused a strange effect (Tab. 1). At these temperatures only the most rapidly growing larvae moulted to L5 or adults while those with a long developmental time eventually died. The selective mortality of slow developing larvae caused a decrease in the average developmental time. As a consequence the developmental time of L4 and L5 at the low temperatures was as long or even shorter than at 28 °C. LDT and SET could not be calculated from these data. Thermal requirements were calculated for L1, L2 and L3 larvae. However, estimated developmental thresholds varied greatly (Tab. 2). Therefore we determined a common development threshold LDT_{L1-L3} = 13.9 °C, using pooled developmental times for L1, L2 and L3 larvae (Fig. 2). The value of this common LDT was near to the value determined from developmental lengths adjusted under the assumption of rate isomorphy (Fig. 3). The values of SET for L4 and L5 instars, total larval and pre-imaginal development were calculated from data collected at 27.8 °C. The SET's were rather high, 556 dd (above LDT_{L1-L3}=13.9 °C) for total larval development, and 742 dd (above LDT_{E-L3}=13.1 °C) for pre-imaginal development (Tab. 2).

DISCUSSION

A comparison of the thermal constants for the development of *Coreus marginatus* with those available for 60 other species of Heteroptera (Honěk & Kocourek 1990, Honěk 1996b) indicate similar values. The average LDT (mean±SD) for Heteroptera eggs was 11.9±3.9 °C (n=63 populations), *for larvae 12.5±3.1 °C (n=64), and for the total development 12.6±3.2 °C (n=63). The LDTs for* Heteroptera development are generally similar to other hemimetabolan orders where species have a large body size. The average LDT for total development in these orders varied between 12.4 °C (Blattodea) and 17.5 °C (Orthoptera). It was, however, lower in small-bodied taxa, aphids (5.2 °C) and Thysanoptera (7.6 °C). The average SET for Heteropteran eggs (113.3±49.7 dd) was not

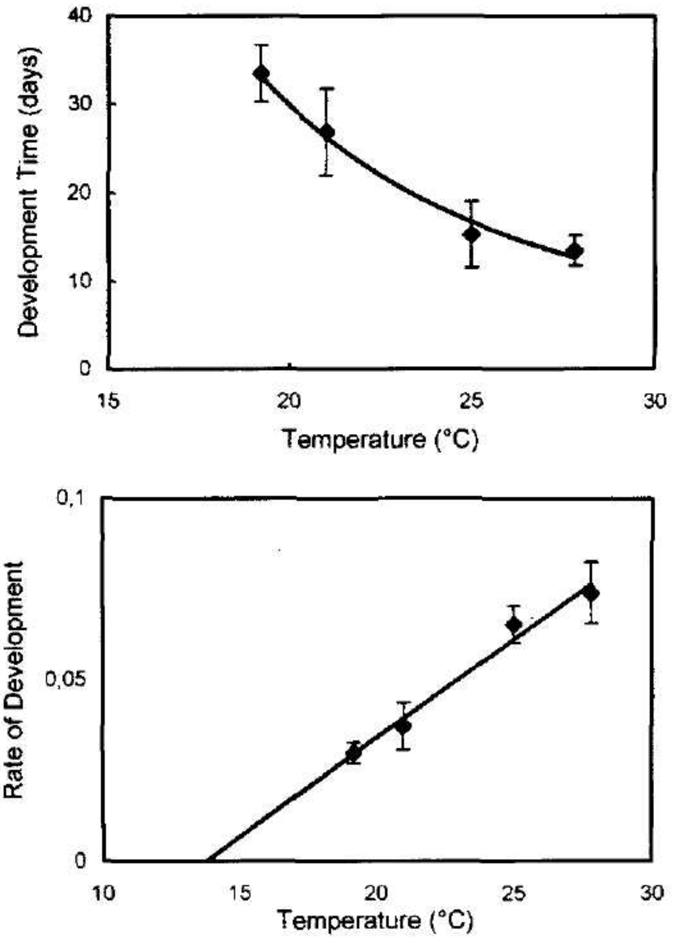

Fig. 2. Pooled developmental duration (above) and developmental rate (below) of L1 - L3 larvae of *Coreus marginatus* at different temperatures. LDT$_{L1-L3}$ = 13.9 °C, SET$_{L1-L3}$ = 185.2 dd.

significantly lower than for *C. marginatus* eggs (142.9 °C). By contrast, average Heteropteran SET for larvae (273.7±118.0 dd) and for total development (368.6±134.1 dd) were substantially smaller than the corresponding values for *C. marginatus*. The high SET of this species was apparently caused by poor food quality.

Feeding *C. marginatus* larvae solely on the seeds of *Rumex obtusifolius* gave poor larval survival at lower temperatures. The mortality of L4 and L5 larvae was rather high. The poor food quality may account for the enormous variation in developmental rate in particular instars, even among larvae that successfully completed the instar. The laboratory reared adults were also generally smaller than those of the parental population from the wild (Hrušková, unpubl.). This was apparently due to poor food, although high average temperature may also contribute to the difference. The reason why a seed diet is not sufficient for the completion of larval development was not established. It might because of the absence of dietary components, available to free living larvae by feeding on green or ripening parts of the host plant or the occasional eating of arthropods (including cannibalism). The suboptimum trophic conditions were best tolerated at the highest temperature of 27.8 °C, where 75 % of the individuals completed their larval development. At lower temperatures only rapidly growing individuals completed their development. The results confirm the effect of the selective mortality of slow growing individuals on the estimates of thermal requirements (Honěk 1999). It causes an apparent increase in the development rate at low temperatures and may be partly responsible for the non-linear course of the development rate/ temperature relationship at these temperatures.

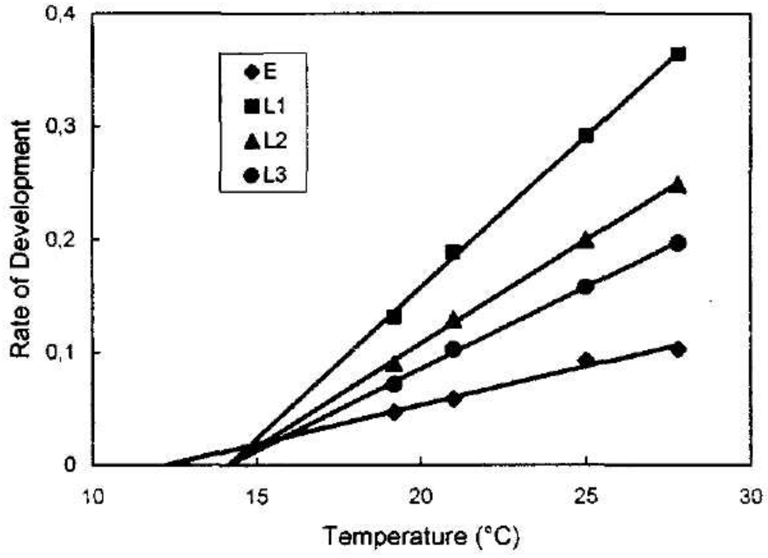

Fig. 3. The regression of the rate of development on temperature for egg (observed data), L1, L2 and L3 instars of *Coreus marginatus* (data recalculated assuming "rate isomorphy" in the larval instars). Thermal constants were LDT = 14.1 °C and SET = 37.4 dd for L1 larvae, SET = 54.7 dd for L2 larvae, and SET = 69.0 dd for L3 larvae. Thermal constants for the eggs are given in Tab. 2.

Acknowledgements

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BOOK REVIEW

LODISH H., BERK A., ZIPURSKI S. L., MATSUDAIRA P., BALTIMORE D. & DARNELL J.: **Molecular Cell Biology**. Fourth edition, second printing. W. H. Freeman, New York, Houndsmills, Basingstoke, 2000. XXXIX+1084 pages, glossary 17 pages, index 36 pages. Format 215×275 mm. Hard cover. Price Lstg 39.95. ISBN 0-7167-3706-X

The author team presents leading authorities – professors affiliated with universities and scientific institutions in California and Massachusetts, and the Rockefeller University. Previous editions occured in print in 1986, 1990, 1995 and 2000. It is pointed up in the preface that modern biology is rooted in an understanding of the molecules within the cells and of the interactions between cells. Since the publication of the third edition of this text in 1995, significant advances and discoveries have been made. The volume is composed of four parts containing 24 chapters in total. Each chapter is divided into numbered subchapters (sections) and is concluded with an overviewing summary, with perspectives for the future and in the literature. An extensive list of references is organized by major section headings. Moreover, to the end of chapters there are questions for self-tests, for reviews, and for challenging data analysis. **Part I: Lying the Groundwork** (chapters 1 through 8) provides insights into basic themes of molecular cell biology. Introducing chapters delineate the dynamic cell and chemical foundations, namely the molecules of life, the cell cycle and architecture, covalent and noncovalent bonds, chemical equilibrium, and biological energy interconversions. In subsequent chapters outlined are protein structure and function, nucleic acids structure and synthesis, biomembranes and the subcellular organization of eukaryotic cells. Concluding chapters describe manipulating cells and viruses in culture, recombinant DNA and genomics, and genetic analysis *in cell biology.* ***Part II:*** *centres attention upon* ***Nuclear Control of Cellular Activity*** *(chapters 9 through 14)* while discussing the molecular structure of genes and chromosomes, notably the chromosomal organization of genes, and morphology and functional elements of eukaryotic chromosomes. Further on, analyzed are regulation of transcription initiation, RNA processing, nuclear transport and posttranscriptional control, DNA replication, repair and recombination, regulation of the eukaryotic cell cycle, and gene control in development. **Part III:** ensures coverage of **Building and Fueling the Cell** (chapters 15 through 19). First, considered is the transport across cell membranes: diffusion of small molecules across phospholipid membranes, membrane transport proteins, various types of membrane transport, membrane electric potential, and osmosis. Next, cellular energetics (glycolysis, aerobic oxidation, photosynthesis) and protein sorting (organelle biosynthesis and protein secretion) are looked at. This part closes with chapters on cell motility and shape – among the topics discussed are the microfilaments including the actin cytoskeleton, the dynamic of actin assembly, myosin, muscle and nonmuscle cells, and the cell locomotion. Finally, attention is devoted to microtubules including microtubule structures and dynamics, kinesin, dynein and intracellular transport, cilia and flagella, microtubule dynamics and motor proteins during mitosis, and to intermediate filaments. **Part IV:** is concerned with **Cell Interactions** (chapters 20 through 24). First chapter of this part offers an overview of cell-to-cell signaling by means of extracellular molecules and receptors. Next examined are nerve cells enclosing neuron structure and function, neurotransmitters, synapses and impulse transmission, and sensory transduction. Final chapters are dedicated to integrating cells into tissues, cell interactions in development, and tumor cells and cancer. Illustrations are one of outstandingly successful point of this publication: featured are - mostly in colour – two- and three-dimensional and space-filling models and arrangements of molecules, internal structures, cross-sectional views and graphical representation of *prokaryotic and eukaryotic cells, biochemical cycles and reactions, diverse diagrams and titration curves, pathways* for energy metabolism and events in biosynthesis, structural formulae, characterization of diverse laboratory procedures, electrophoretic, chromatographic, separation, fractionation, purification, and other procedures, light and electron microphotographs, fluorescent images, genetic processings, chromosomal mapping, dendrograms, and many more. Some figures provide presentation of computer-generated images based on known models of organelles. In addition, there are numerous tables offering overviews of presented data. A study companion affiliated with the presented publication there is the *Working with Molecular Cell Biology*, fourth edition, written by B. Storrie, M. Lederman, E. A. Wong, R. A. Walker and G. Gillaspy (all from Virginia Polytechnic Institute and State University) – published by W. H. Freeman in 2000. Another study companion there is a CD-ROM packaged with every copy of the textbook which contains all art from the text, plus animations and videos. The figures in the book and their related animations use a consistent colour scheme. The CD and the book can be used together without confusion. Outstandingly successfull point of this publication there is vizualization of cell and molecular processes which helps students better understand the relationship between structure and function.

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Timing of diapause induction in the cabbage bug *Eurydema rugosum* (Heteroptera: Pentatomidae) on different host plants

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Abstract. In the field, first generation adults of *Eurydema rugosum* Motschulsky, 1861 (Heteroptera: Pentatomidae) emerged in early summer and most entered diapause on brown mustard plants that bloomed in early spring and died by early summer. On cultivated crucifers, which had green leaves all year round, however, most adults of the first generation reproduced and the second generation that emerged in late summer entered diapause. Under the quasi-natural photoperiod and temperature conditions that prevailed when the first generation developed in the field, most adults raised on seeds of oilseed rape entered diapause whereas most adults raised on leaves of the same plant reproduced. Under the quasi-natural photoperiod and temperature conditions that prevailed when the second generation developed in the field, most adults raised on leaves entered diapause. Thus, *E. rugosum* shows either a univoltine or bivoltine life cycle, depending on the phenology of the host plants.

Adult diapause, host plant, Brassicaceae, photoperiod, life cycle, Heteroptera, Eurydema rugosum

INTRODUCTION

It is our pleasure to contribute an article to this memorial issue of the Acta Societatis Zoologicae Bohemicae dedicated to the occasion of the 70th birthday of Dr Ivo Hodek.

Diapause plays an important role in the life cycle of many insects (Tauber et al. 1986, Danks 1987). The primary cue for the induction of diapause, is photoperiod, although other environmental factors such as temperature, food, humidity or density sometimes modify the photoperiodic response (Tauber et al. 1986, Danks 1987). In phytophagous heteropterans, photoperiod predominantly determines the induction of diapause (e.g. Hodek 1968, Numata & Hidaka 1982, Higuchi 1994, Nakamura & Numata 1997), although temperature also plays a major role in *Dybowskyia reticulata* (Dallas, 1851) (Nakamura & Numata 1998). Dietary factors as well as humidity and density have attracted limited attention.

The cabbage bug *Eurydema rugosum* Motschulsky, 1861 (Heteroptera: Pentatomidae) is an oligophagous species feeding on several crucifers (Tomokuni et al. 1993). In this species, not only photoperiod but also dietary conditions play an important role in the induction of diapause: Insects raised under long-day conditions on leaves of oilseed rape become reproductive adults, whereas those raised under long-day conditions on seeds of the same plant and those raised under short-day conditions on seeds or leaves become diapause adults (Numata & Yamamoto 1990). From these results, Numata & Yamamoto (1990) suggested that *E. rugosum* uses the status of the host plant as a cue for timing the induction of diapause.

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Yano & Ohsaki (1993) observed the phenology of various wild crucifers in the field in Kyoto City, Japan. Some species bloom in early spring, their seeds mature, and the whole plants die by late spring or the above-ground parts of most individuals die in early summer. Thus, in these species the vegetative parts disappear during summer. The other species have green leaves all year round, and are a continuous potential food source for insects. Our preliminary observations showed that many adults of *E. rugosum* feed on plants of the former group such as the brown mustard, *Brassica juncea* Coss., in spring, and some adults feed on cultivated crucifers in summer as well as in spring. However, it is unclear how *Eurydema rugosum* responds to the status of these host plants under natural conditions to adapt its life cycle to the phenology of the host plants.

The present study was performed to clarify the timing of diapause induction in *E. rugosum* on different host plants. For this purpose, we observed the development of *E. rugosum* on brown mustard in the field and the phenology of this plant, examined the reproductive status of adults collected from different host plants at different times of the year, and reared *E. rugosum* from eggs under quasi-natural photoperiod and temperature conditions.

MATERIALS AND METHODS

Observation and collection on brown mustard

From April 1987 to April 1988, changes in *Brassica juncea* and the development of *E. rugosum* on this plant were observed in the field in Tawaramoto (34° 30' N, 135° 45' E), Nara Prefecture, Japan, at 5–10 day intervals. If found, adults of *E. rugosum* were collected. One day after collection, some females were dissected and the developmental stage of their ovaries determined.

The remaining adults were reared as male/female pairs in plastic cups (200 ml) under a photoperiod of 14-h light and 10-h darkness (LD 14:10) at 20 ± 1 °C for 33 days. Brown mustard plants collected from the field together with the insects were provided as food. Oviposition was recorded daily. The females that did not lay eggs were dissected, and the stage of development of the ovaries was determined.

Collection on cultivated crucifers

Adults of *E. rugosum* were collected at about 7-day intervals from June to September 1989 in vegetable plots in Tawaramoto or Kyoto City (35° 00' N, 135° 45' E), Japan, where green leaves of cruciferous crops existed throughout this period. They were reared as male/female pairs in plastic cups (200 ml) on leaves of oilseed rape *Brassica napus* L. for 30 days under conditions of quasi-natural photoperiod and temperature in Osaka City (34° 41' N, 135° 31' E), i.e., on an upstairs hallway of our building with several windows, no artificial light and no air conditioning. The reproductive status of the females was determined as described above.

Rearing under quasi-natural photoperiod and temperature

Adults of *E. rugosum* were collected on brown mustard and cabbage *Brassica oleracea* var. *capitata* L. in May and July 1989, respectively, and their progeny were reared on dried seeds or seedling leaves of oilseed rape under conditions of quasi-natural photoperiod and temperature as described above. The first-instar nymphs were supplied only with water, and food was supplied from the second instar. Leaves and seeds were replaced daily and at about 5-day intervals. Water was also supplied for the insects fed seeds. The density of nymphs was maintained from the second instar at about 12 per plastic cup (200 ml). After adult emergence, insects were reared as male/female pairs in plastic cups (200 ml) for 20 days. The females that did not lay eggs and the males that did not mate were dissected. The females with yolk deposition were judged to be nondiapause adults, as were those that laid eggs. In males, when the ectodermal sac of the accessory gland was filled with secretory fluid, the insects were judged to be nondiapause adults, as were those that mated (Numata & Yamamoto 1990).

RESULTS

1. Seasonal changes in brown mustard plants and the reproductive status of *E. rugosum*

We found the first adults of *E. rugosum*, which had overwintered on flowering brown mustard in early April, eggs in late April, when the flowers of brown mustard had withered, first-instar nymphs from early May to early June, second-instar nymphs from late May to mid-June, third-instar nymphs from late May to late June, fourth-instar nymphs from the end of May to early July, and fifth-instar nymphs from early June to July (Fig. 1). Brown mustard produced seed during nymphal development of the first generation. We found newly emerged adults from mid-June, when the seeds of brown mustard was being shed (Fig. 1). Soon after emergence, most of these adults left the plants and thereafter only a few adults were found there.

The preoviposition period became shorter as the collection date advanced from early to mid-April. On April 19, the median preoviposition period was only three days (Fig. 1). Thus, adults that had overwintered began to lay eggs in mid-April. When adults were collected on April 9, 14 and 19, 44 of 46 females had vitellogenic oocytes, and all of 155 females collected between April 24 and June 8 had vitellogenic oocytes. The median preoviposition period of the females collected between April 24 and June 8 was three days or less (Fig. 1). Thus, overwintering adults survived to June and continued to lay eggs until mid-June.

Some adults collected in mid-June had soft cuticles, showing that they had recently a few days after emerged. One of the 9 females collected on June 13 had no vitellogenic oocytes. After those collected on June 18, 5 of 6 females had no vitellogenic oocytes, and females collected on the same day did not lay eggs for 33 days. Twenty-one of 23 females collected on June 23 also had no vitellogenic oocytes. Thereafter, most females did not lay eggs for 33 days. In this experiment no females began to lay eggs between 30 and 33 days after transfer to laboratory conditions, and all females that did not lay eggs for 33 days had no vitellogenic oocytes and well-developed fat bodies, indicating that they were in diapause. In late June and July, most females were in diapause (Fig. 1). From June 28, we checked the spermatheca of dissected females, to determine whether they had mated. More than 90 % of the females collected on and after June 28 (total n = 39) had no

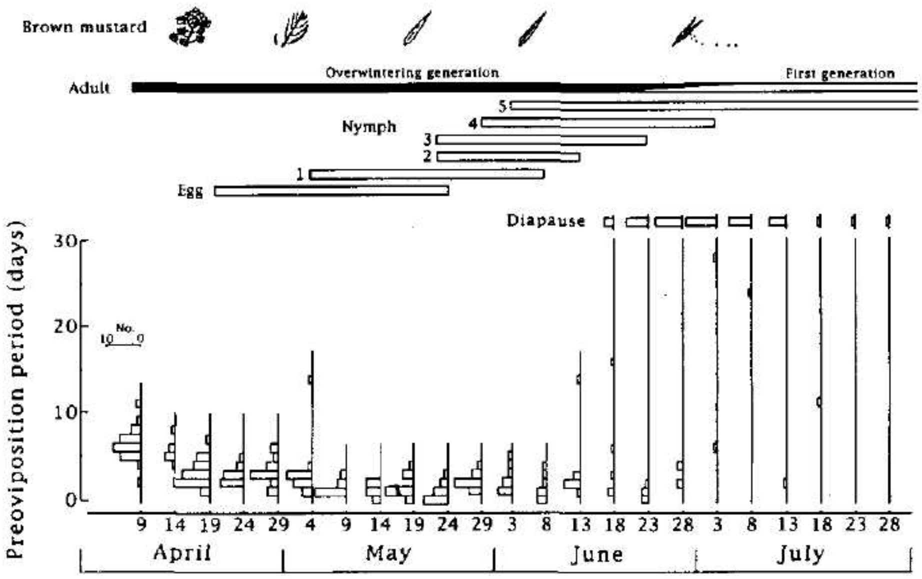

Fig. 1. Seasonal changes in the development of the brown mustard, and of *Eurydema rugosum* Motschulsky on this plant in Tawaramoto in 1987, and the preoviposition period of adults collected at different times from April to July and kept under LD 14:10 at 20 °C. Brown mustard plants were supplied as food.

vitellogenic oocytes and no spermatozoa. Thus, most adults of the first generation of the year that developed on brown mustard entered diapause.

In mid-July, there were many seedlings of *Brassica juncea* in sunny places where old plants had withered. However, most of these seedlings died and the surviving plants did not grow, probably because of hot and dry conditions that prevailed during the summer and consumption by other phytophagous insects. From mid- to late July, we found only few adults and fifth-instar nymphs on withered plants. Thereafter we found no nymphs, and only few adults were found on seedlings of brown mustard. After finding one adult female on October 11, we did not find *E. rugosum* again until March 28 the next year. In early October, after the grass was artificially cut, seeds of *B. juncea* germinated synchronously. These plants grew gradually during autumn and winter, and in February some bolted. In mid-March, all plants bolted and produced flower buds. We first found 2 male adults on March 28. Then, although we observed for 90–150 min every day, but found only a few adults per day. On April 3 when most of the plants were in flower, however, we collected 111 adults in 90 min.

In 1987, we did not discriminate newly emerged adults based on their cuticle hardness. On July 17 and 23, 1989, we collected adults of *E. rugosum* again on brown mustard and dissected them. All the females were new adults and only 1 of 33 females had vitellogenic oocytes.

2. Seasonal changes in the reproductive status of *E. rugosum* on cultivated crucifers

In this experiment, we checked the hardness of the cuticules of all collected adults on the day of collection to determine whether they were newly emerged.

When adults of *E. rugosum*, collected in plots of radish *Raphanus sativus* var. *hortensis* Backer in mid-June, were kept under quasi-natural conditions, they began to lay eggs within four days (Fig. 2A), similarly to those collected on brown mustard at the same time (Fig. 1). New adults emerged from late June. More than half of the females collected on June 26 and July 3 had soft cuticles and were identified as new adults. None of the new females collected on July 3 and had vitellogenic oocytes (n = 14). However, most of the new females began to lay eggs without entering diapause under quasi-natural conditions, although their preoviposition period was much longer than that of old females with hard cuticles. A small proportion of the new females did not lay eggs for 30 days (Fig. 2A). In this experiment all females that did not lay eggs for 30 days had no vitellogenic oocytes but well-developed fat bodies, indicating that they were in diapause. The radish bolted in June, and was harvested before producing seeds in early July. Thereafter, we collected *E. rugosum* in plots of cabbage near to the above-mentioned plots of radish.

On July 10 and 17, we found mostly new adults. Only 3 of 22 new females had vitellogenic oocytes. However, a greater proportion of the females collected on July 10 and 17 began to lay eggs after 5–18 days under quasi-natural conditions. All adults collected from July 30 to August 14 were probably of the first generation of the year, because the proportion of new adults increased from late June and all adults collected in mid-July were new. Their preoviposition period was shorter than that of the females of the first generation collected in early July (Fig. 2A).

We found some new adults again on plots of cabbage in Tawaramoto from late August to early September, and they were probably of the second generation of the year, because adults that were assumed to be of the first generation laid eggs in late July and August. We observed fewer adults in September than in July and August, and most of these adults entered diapause (Fig. 2A). During the observation period in July and August, cabbage did not bolted.

We collected adults of *E. rugosum* from plots of radish in Kyoto on August 4. All 16 females collected began to lay eggs within 5 days under quasi-natural conditions. We collected some adults on radish plants in Kyoto on September 16. None of these females laid eggs and they were all in diapause (Fig. 2B).

Therefore, the progeny of overwintering adults of *E. rugosum*, i. e. the first generation of the year, became mostly nondiapause adults when reared on cruciferous plants with green leaves in summer. Adults of the second generation entered diapause when reared on such plants.

3. Effects of diet on the induction of diapause under quasi-natural photoperiod and temperature

In the first experiment, we reared the adults collected from brown mustard under LD 14:10 at 20 °C. These conditions are similar to those in nature in late April or early May, and female adults that had already begun oviposition continued regardless of the type of food supplied under these conditions (Ikeda-Kikue & Numata 1992). If a field-collected adult is reproductive, it will not enter

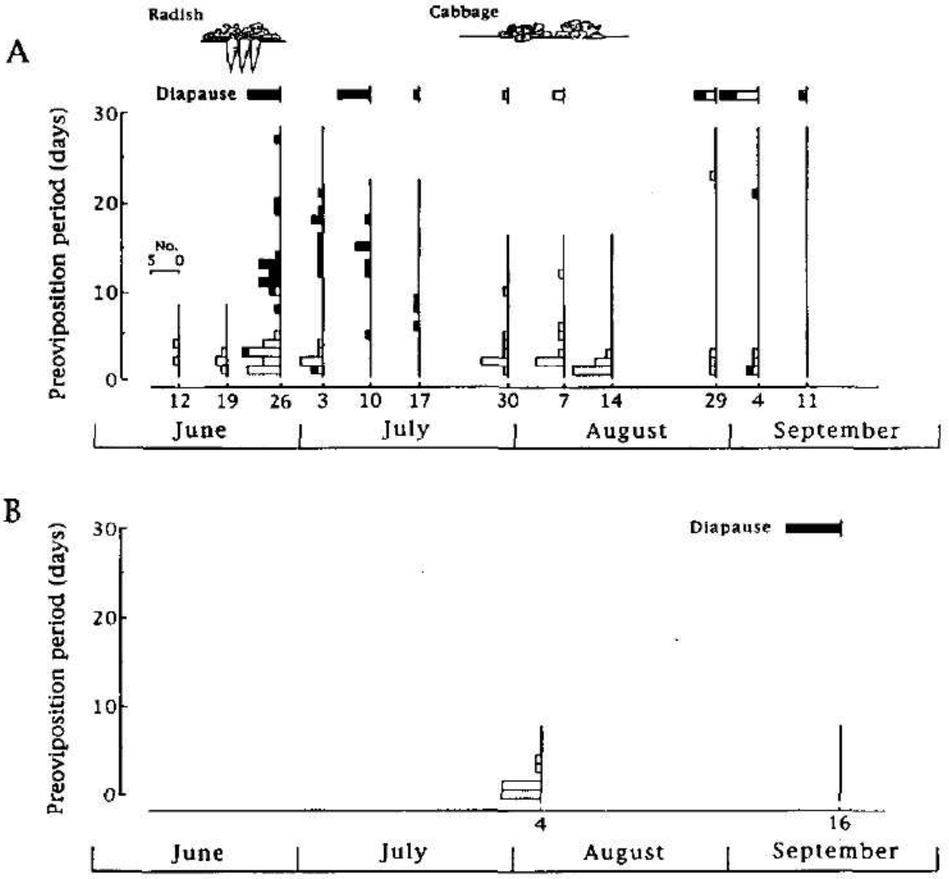

Fig. 2. Seasonal changes in the preoviposition period, under quasi-natural photoperiod and temperature conditions, of adults of *Eurydema rugosum* Motschulsky collected on cultivated crucifers in Tawaramoto (A) and Kyoto (B) in 1989. Solid bars indicate newly emerged adults with soft cuticles. Leaves of oilseed rape were supplied as food.

diapause under these conditions. We assumed, therefore, that the reproductive status of field-collected adults kept under these conditions reflects that under natural conditions. In June and July, however, natural temperature was higher and daylength longer than in the laboratory. Therefore, we could not exclude the possibility that adults transferred from the field to LD 14:10 at 20 °C entered diapausing response to an artificial decrease in temperature or daylength. Therefore we reared insects under the conditions of quasi-natural photoperiod and temperature, when the first generation grew, on seeds or leaves to examine whether these dietary conditions can induce or avert diapause.

We placed eggs of *E. rugosum* under quasi-natural conditions in early May, when adults after overwintering reproduced on brown mustard in the field (see Fig. 1). The duration of the egg stage was about 7 days in this season. Adults emerged in late June both on seeds and on leaves of oilseed rape. All adults raised on seeds survived for 20 days, and all except one female entered diapause (Fig. 3). Although about 25% of the adults reared on leaves died within 20 days after emergence, most of the surviving females began to lay eggs 11 to 20 days after emergence, and about 70 % of surviving males were reproductive (Fig. 3). Thus, in early summer, diapause was induced in insects fed on seeds but not in those fed on leaves. The mortality rate was lower in insects fed on seeds than in those fed on leaves.

Next, we placed eggs of *E. rugosum* under quasi-natural conditions in late July, when adults of the first generation laid eggs in vegetable plots in the field (Fig. 2A). Nymphs and adults were fed on leaves. Adults emerged from late August, when the adults of the second generation emerged in the field (Fig. 2A). Although 50 % of adult females died without oviposition within 20 days after emergence, the surviving females ceased ovarian development and entered diapause, with a single exception. This exceptional female did not lay eggs for 20 days but on dissection was found to have vitellogenic oocytes. About 40 % of adult male died without mating and most of the surviving males entered diapause (Fig. 3). Thus, in late summer insects fed on leaves entered diapause.

DISCUSSION

Life cycles of phytophagous insects are dependent on the phenology of their host plants (Tauber et al. 1986, Danks 1987). In some crucifers, whole plants or the above-ground parts disappear during summer, when many phytophagous insects are active (Yano & Ohsaki 1993). Yano & Ohsaki (1993) regarded this seasonal disappearance as a defense mechanism for avoiding utilization by phy-

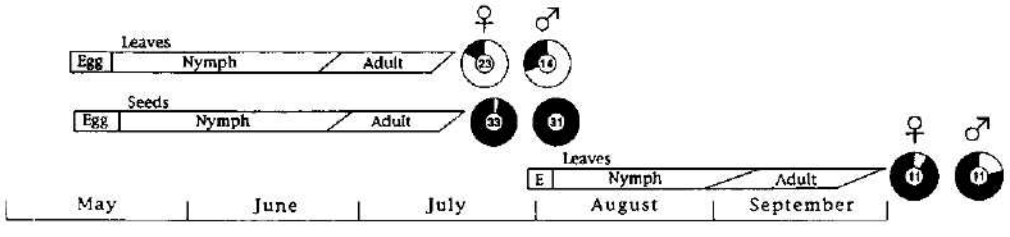

Fig. 3. Incidence of adult diapause in *Eurydema rugosum* Motschulsky kept under quasi-natural photoperiod and temperature cobditions on different diets. Numerals in fan diagrams indicate sample sizes. Solid fan, diapause; open fan, reproduction.

tophagous insects, and concluded from their field observations that polyphagous insects that feed on these plants accidentally or monophagous insects that have evolved counter strategies for the seasonal disappearance can utilize this type of crucifers. Among three species of coexisting sawflies feeding on crucifers, utilization of host plants is different. Cardamine plants sprout in spring and autumn, showing seasonal disappearance. *Athalia japonica* (Klug, 1915), which mainly uses Cardamine plants, enters a summer diapause in the prepupal stage. However, *Athalia rosae ruficornis* Jakovlev, 1898 and *Athalia infumata* (Marlett, 1898) primarily use host plants with new leaves all year round, and lack summer diapause (Nagasaka 1992a).

A. rosae ruficornis utilizes cultivated crucifers. The amount of cultivated crucifers decreases at low altitudes in summer, and adults of this species take a countermeasure against this food shortage by migration. On the other hand, adults of *A. infumata* disperse to seek temporary host plants, the yellow cress *Rorippa indica* (L.) (Nagasaka 1991, 1992b). The present results indicate that diapause in *E. rugosum* is induced at different times of year on different host plants, and thus phenology of host plants affects the life cycle of *E. rugosum*. We did not examine migration or dispersal of *E. rugosum*. However, diapause induced on seeds under long-day conditions is not terminated by supplying leaves as food (Ikeda-Kikue & Numata 1994). Therefore, it is unlikely that diapause adults of the first generation, which have developed on brown mustard, migrate to other host plants and produce a second generation there.

Thus, *E. rugosum* shows either a univoltine or bivoltine life cycle, depending on the phenology of the host plants. When adults after overwintering laid eggs on host plants that bloom in early spring, and the whole plants die by early summer, most adults of the first generation entered diapause. On the other hand, when adults after overwintering laid eggs on host plants with green leaves all year round, most adults of the first generation averted diapause and produced the second generation, and all adults of the second generation entered diapause. As the progeny of the same parents collected from brown mustard entered and averted diapause on seeds and leaves, respectively, in three independent experiments (Numata & Yamamoto 1990, Ikeda-Kikue & Numata 1994, Fig. 3), it is unlikely that there were two genetically different populations in *E. rugosum* and these two populations showed different voltinism on different host plants.

As *A. japonica* adapts its life cycle to the phenology of *Cardamine* plants (Nagasaka 1992a), *E. rugosum* primarily regulates its life cycle to coordinate the phenology of host plants like *B. juncea*. However, this insect does not feed exclusively on crucifers with seasonal disappearance, because adults of the first generation reproduce on crucifers without seasonal disappearance. Many univoltine insects utilize host plants usable during only a restricted period of the year (e.g., Slansky 1974, Ishii & Hidaka 1982, see also Saulich & Volkovich 1996). The phytophagous pentatomid bug *Graphosoma rubrolineatum* (Westwood, 1873) has a univoltine life cycle in Osaka, where its food, seeds of Umbelliferae, are produced only within a limited period, even though this species has not completely lost the photoperiodic response (Nakamura & Numata 1999). If the fraction of density-independent rate of annual increase by producing a second generation exceeds the survival rate during diapause of a univoltine life cycle, a bivoltine life cycle is favored over a univoltine one (Sota 1988). We have not examined the survival rate during diapause in both types of life cycles in *E. rugosum*. However, if we assume the rate does not differ considerably, it is of great adaptive significance that *E. rugosum* produces an additional generation when adults after overwintering lay eggs on host plants with phenology different from that of brown mustard. Unless mortality during diapause differs considerably, a bivoltine life cycle is favored over a univoltine life cycle (Sota 1988). It is, therefore, of great adaptive significance that *E. rugosum* produces an additional generation when adults after overwintering lay eggs on host plants with phenology different from that of brown mustard.

In many phytophagous insects, dietary conditions have been shown to affect the induction of diapause. Diapause response of a species sometimes differs when it feeds on different plant species (Tauber et al. 1986, Danks 1987). For example, Hunter & McNeil (1997) reported that in the polyphagous obliquebanded leafroller, *Choristoneura rosaceana* (Harris, 1864), host plant species influenced the induction of larval diapause and voltinism. In *E. rugosum*, however, host plant species did not directly affect the induction of diapause. A combination of a long-day photoperiod and seeds as food induces diapause regardless of whether the seeds are of oilseed rape or brown mustard (Numata & Yamamoto 1990, figs. 1, 3), and a combination of a long-day photoperiod and leaves as food induces reproduction regardless of whether the leaves are of oilseed rape or radish (Numata & Yamamoto 1990, figs. 2, 3). In *E. rugosum*, therefore, it is not the species but the developmental state of host plants that plays a definitive role in the induction of diapause under long-day conditions (Numata & Yamamoto 1990, fig. 3).

In general, less nutritious diets tend to induce diapause (Tauber et al. 1986, Danks 1987). In *C. rosaceana* also, diets of nutritionally lower quality induce diapause (Hunter & McNeil 1997). In *E. rugosum*, however, dietary conditions favoring diapause were not nutritionally inferior, because the survivorship and weight gain in the nymphal period are higher on seeds than leaves under constant conditions (Numata & Yamamoto 1990). The mortality was higher on leaves than seeds in the present study under quasi-natural conditions. In the codling moth *Cydia pomonella* (Linnaeus, 1758) induction of larval diapause is primarily controlled by photoperiod but is also influenced by the maturity of the host fruit (Jermy 1967, Sáringer 1977, El-Gamil et al. 1978, Steinberg et al. 1992). Adult diapause of the boll weevil *Anthonomus grandis* Boheman 1843 is also chiefly controlled by photoperiod, but its incidence is increased by feeding on mature fruit rather than flower buds or young fruit of cotton plants (Lloyd et al. 1967, Tingle & Lloyd 1969). In these cases, a dietary factor functions as a signal indicating conditions of a single plant species. In *E. rugosum*, the developmental state of host plants also physiologically determines the induction of diapause, overriding the photoperiodic response. The developmental state of host plants is an indicator of the life cycle pattern of the host plants to *E. rugosum*, and enables the insect to adapt appropriately.

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TOMOKUNI M. YASUNAGA T., TAKAI M., YAMASHITA I., KAWAMURA M. & KAWASAWA T. 1993 [*A Field Guide to Japanese Bugs – Terrestrial Heteropterans*]. Tokyo: Zenkoku Noson Kyoiku Kyokai, 381 pp (in Japanese).

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BOOK REVIEW

KOMÁREK S. 1998: **Mimicry, Aposematism and Related Phenomena in Animals and Plants. Bibliography 1800–1990.** Vesmír, Prague 1998, 296 pp. (Distributed by Kabourek, s. r. o., Sokolská 3923, CZ–76001, Zlín, Czech Republic. Price not stated.)

No bibliography of the phenomena mentioned in the title has ever been compiled, and S. Komárek's work admirably fills the gap. The book includes brief introductory parts (general comments on the aim, scope and format of the work; a short discourse on the nature of the mimetic phenomena attempting to cast some doubts on the purely selectionist explanations by neodarwinists; list of some 115 abbreviations used in annotations and indexes), and two alphabetically arranged and separately numbered annotated bibliographies including 4767 references concerning animals and 471 concerning plants and fungi. The bibliography is concluded by many useful but idiosyncratically arranged indexes extending over 57 pages.

The core of the book are the bibliographies attempting to cover in full particularly the older and non-English literature which could easily fall in oblivion in the age of computerized retrieval of modern and mainly Anglo-American sources. The author has had to draw the the lines somewhere – the vast subject would otherwise prove untractable or too patchily covered. The works on Batesian, Muellerian, Peckhamian and partial mimicry, aposematism, and the most extreme forms of crypsis are fully covered. Works on coloration and color changes associated purely with SMRSs and adjustments to the environment, on industrial melanism and acoustical mimesis are excluded (the latter in order to avoid too abundant literature on imitation of songs in birds).

The annotations are accompanying all the references, and are uniformly structured, providing information on the biogeographical region, names and classification of the mimic and the model (if known), kind of adaptive coloration, and nature of the work. The indexes are extremely useful, cover a variety of aspects, and form jointly a large cross-referenced subject-index whose compilation must have been almost as time-consuming as that of the bibliography itself. The organization of indexes is unfortunately not self-evident and has to be learned; however, those who are interested and patient enough will be rewarded by a wealth of information not obtainable by other means. The major obstacle for an easy use of the indexes is a usage of too many abbreviations even in key entries, a shortcoming which could have been easily avoided by extending the index by a couple of extra pages.

What I miss is a simple glossary of major terms concerning mimesis and related phenomena; not all of those used do belong to the thesaurus of an average biologist; a few others could have been added to make the list nearly complete. Considering that the author has examined so many general papers and all comprehensive monographs it seems a pity that the works on the acoustic mimesis has been omitted completely ; only the birds and mammals could have been exluded, and the literarure on other animals covered. The phenomenon is infrequent (at least thought so) but often pretty bizarre and evolutionarily important. The same applies to ever more important subject of chemical mimesis (e.g., essential for understanding social parasitism in ants, wasps and bees), though, admittedly, a full coverage of this subject would require a cooperation with a chemical ecologist, and I would be at pains to approach it in plants and fungi. However, it seems to me that the author's passion for completeness has in the two latter cases overcome his awareness of utility (on the other hand, it seems cheap to criticize purposeful exclusions instead of prizing what has been done in full).

The author is to be congratulated for providing a unique, excellent, and reliable bibliography of mimicry and aposematism; it will become a fundamental and permanent source of information for all the students of these phenomena. I should like to emphasize three general points as well. First: Such specialized bibliographies probably cannot ever be replaced by any computerized databases since the compilation of the former requires enthusiasm as well as knowledgeable selection, rejection and evaluation of published texts rather than blind search for a few combinations of key-words which cannot cover the possibly important ideas nad hypotheses published *en passant*. Second: Only through such an historically minded and linguistically unbiased approach the wealth of data and thoughts of our predecessors can be preserved, and both utilized and honoured. Third: Komárek's bibliography apperars in a time when an interest in this evolutionary and ethological evergreen becomes a hot topic again. The reasons? "Evolutionarization" of ecology and ethology; advantages following from applications of modern cladistic techniques to old problems in comparative biology; realization of necessity of attempting to get rid of anthropocentric assessments of mimetism and aposematism; integrative trends in modern systematic biology (e.g., entomology *cum* ornithology relative to the significance of warning colours in insects).

I can only hope that the opportunities offerred by this bibliography will be fully exploited.

Pavel Štys

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Hibernation of *Harmonia axyridis* (Coleoptera: Coccinellidae) in South-Eastern France

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Abstract. *Harmonia axyridis* (Pallas, 1773), an exotic and polyphagous ladybird was introduced into France as a biological control agent for use against Homoptera. It can be produced on a large scale using a substitute prey the eggs of *Anagasta kuehniella* (Zeller, 1877) which make it an ideal choice for numerous applications in biological control. In order to determine whether adults can survive outside over winter an experiment was started in 1993 at 5 sites in the mountains and hills in South Eastern France. The coccinellids survived well at all five sites. While monitoring these hibernating beetles their physiological condition and the intensity of their dormancy were recorded monthly.

Hibernation, dormancy, Coleoptera, Coccinellidae, *Harmonia axyridis*, France

INTRODUCTION

Harmonia axyridis (Pallas, 1773), an exotic ladybird from eastern Asia, is a polyphagous predator that attacks many species of homopterous insects especially aphids (Iablokoff-Khnzorian 1982). It is a prospective candidate for biological control and was recently introduced into the North Eastern USA and the South-East of France. Where it is native, for exemple, Japan, the adults migrate every year to hibernation sites, and aggregate during winter at prominant features of the landscape (Obata et al. 1986). The most important difficulty experienced in acclimatizing this species to a new area appears to be its low ability to survive during winter (Mc Clure 1987). An experiment was started in 1993 to determine the survival of adults hibernating on mountains and hills in the South East of France.

MATERIAL AND METHODS

This study of the hibernation of *H. axyridis*, in South Eastern France was done using beetles reared under natural conditions in Antibes in the month of September and fed on abundant supply of eggs of *Anagasta kuehniella* (Zeller, 1877). Decreasing temperature (< 22°C) and photoperiod (< 14:40 hours) acting on the preimaginal stage induce imaginal diapause in December (Ongagna & Iperti 1994). These adults were placed in traps at 4 hibernation sites in the Southern Alps (Rocher de Roquebrune, Alpilles, Courbons, Col du Tourniol) and in Antibes (Tab. 1). Tab. 2 summarises the details of the sites, the dates, the ages and numbers of ladybirds used. Every month these sites were visited to determine the physiological condition of the hibernating adults, the intensity of their dormancy and to observe their reactivation and spring emergence.

RESULTS AND DISCUSSION

The physiological condition of the coccinellids was determined by dissecting monthly 10 males and 10 females from each site until spring emergence. Criteria recorded were size of fat body, content of mid gut, activity of ovaries and contents of spermathecae in the females and seminal vesicles in

Tab. 1. Conditions experienced by larvae of *Harmonia axyridis* (Pallas) during their outdoor development in Antibes

larval stage (dates)	length of larval stage (day)	temperature (°C)	photoperiod (H)
beginning 12/08	19 + 2	22.5	15h 18
end 01/09			14h 13
beginning 17/08	20 + 2	22.0	15h 03
end 07/09			13h 50
beginning 23/08	21 + 2	22.2	14h 40
end 13/09			13h 41

males. The results are summarised in Tab. 3. In December in Rocher de Roquebrune, Alpilles and Courbons the fat body is large in most adults and begins to get smaller in February. Over the same period the digestive track is empty and ovaries are immature except for 10% that are regressed. Up to February most spermathecae are empty and start to become filled in March and especially April. The follicular tissue in males remains active in resting individuals. The results for adults from Col du Tourniol are a little different. The fat body was smaller at the beginning of hibernation and the spermatecae of a greater number of females were full of spermatozoids.

The intensity of hibernation was measured by the average preoviposition period of 10 pairs collected monthly from each site and fed *ad libitum* with the eggs of *A. kuehniella* and kept at 22 ± 1°C and under a 16 hours daily ligth regime (Tables 4 and 5). The duration of the preoviposition period was greater than 11 days from November to February, with a maximum of 16 days in December. It decreased after January and was 7 days in March. The beetles from the Rocher de Roquebrune followed the same trend as those in Antibes, being an average of 12 days in January and 7 days in March. In the beetles from the Alpilles, reactivation was slower up to the beginning of March, when it was an an average of 12 days, and then became more normal with average of 8 days at the end of March. At Courbons and the Col du Tourniol it was respectively, April and May before the reactivation occurred and took an an average of 7 days.

The spring emergence seems to be dependent on ambient temperature (Hodek & Honěk 1996), the threshold of an activity always being above 10°C even in temperate regions (Iablokoff-Khnzorian 1982). On the 9th April at the Rocher de Roquebrune only 15 adults were found, which

Tab. 2. Characteristics of the hibernating sites

site	groups	altitude (m)	latitude (°)	date*	number of adults	age of adults (days)
Antibes	I	40	43.5	from 1. 9. 1992	2245	from the beginning
	II	40	43.5		2020	
Rocher de Roquebrune (Var)	III	280	43.5	9.12.1992	1500	90
Alpilles (Bouches du Rhone)	IV	230	43.5	16.12.1992	1690	100
Courbons (Digne Alpes de Haute-Provence)	V	1200	44.0	23.12.1992	1818	100
Col de Tourniol (Valence, Drome)	VI	1180	45.0	10.1.1993	1788	120

* when beetles were placed at site

Tab. 3. Results of the dissections (% of adults) made on coccinellids Harmonia axyridis (Pallas) collected at the different hibernating sites. Legend: F = full; l = small; Im = immature; E = empty; m = medium; M = mature; L = large; R = regressed

sex	females										males						
month	midgut		fat body			spermatheca		ovaries			midgut		fat body			seminal vesicle	
	F	E	l	m	L	E	F	Im	M	R	F	E	l	m	L	E	F
Roquebrune																	
Dec.	30	70	10	10	80	90	10	90	0	10	10	90	0	10	90	80	20
Jan.	0	100	0	10	90	70	30	100	0	0	0	100	10	30	60	80	20
Febr.	0	100	0	70	30	100	0	100	0	0	0	100	30	0	70	80	20
March	0	100	10	30	60	90	10	100	0	0	0	100	44	0	56	100	0
April	0	100	90	10	0	10	90	70	0	30	0	100	10	0	0	100	0
Courbons																	
Dec.	20	80	10	20	70	78	22	100	0	0	30	70	0	40	60	40	60
Febr.	0	100	0	30	70	100	0	100	0	0	0	100	0	0	100	80	20
March	0	100	0	60	40	70	30	100	0	0	0	100	10	70	20	100	0
April	0	100	100	0	0	40	60	80	20	0	0	100	90	10	0	100	0
March	0	100	90	10	0	23	77	56	44	0	0	100	100	0	0	100	0
Alpilles																	
Dec.	50	50	20	40	40	50	50	90	0	10	100	0	20	50	30	90	10
Jan.	0	100	0	37	63	50	50	100	0	0	0	100	0	20	80	80	20
Febr.	0	100	50	10	40	100	0	100	0	0	0	100	20	10	70	80	20
March	0	100	40	0	60	50	50	100	0	0	0	100	11	11	78	100	0
April	30	60	90	10	0	25	75	100	0	0	0	100	100	0	0	100	0
Tourniol																	
Jan.	25	75	50	50	0	25	75	100	0	0	20	80	60	20	20	60	40
Febr.	0	100	33	33	34	66	34	100	0	0	0	100	20	0	80	80	20
March	0	100	0	40	60	50	50	70	30	0	0	100	0	80	20	100	0
April	0	100	0	100	0	20	80	60	40	0	0	100	10	70	20	100	0
May	20	80	100	0	0	10	90	40	60	0	10	90	100	0	0	100	0

indicated the adults dispersed in March. Only 2.5 % of the ladybird were died during hibernation. Most adults dispersed from Alpilles in April because on 14th April only 400 individuals were present (2 % of the ladybirds died during hibernation). The coccinellids left the Col de Tourniol site at the beginning of May because on the 22 May only a hundred coccinellids were discovered.

Tab. 4. Average duration of preoviposition period (days) of adults at 22 + 1°C and a 16 hour-day length and fed on abundance of eggs of *Anagasta kuehniella* (Zeller)

dates \ sites	Antibes	Roquebrune	Alpilles	Courbons	Tourniol
November	11(19–7)+1				
December	16(20–12)+1				
January	14(24–10)+1	12(17–7)+2	14(18–11)+2		
February	9(12–7)+1	11(13–10)+1	12(14–9)+1	11(14–8)+1	11(13–8)+1
beginning of March		9(10–6)+1	12(17–11)+1	13(14–12)+1	13(18–10)+2
end of March	7(10–4)+1	7(9–6)+1	8(12–6)+1		
April				7(12–4)+2	9(11–7)+1
March					7(13–5)+1

Tab. 5. Statistical comparison of the average preovipostion periods each month of females of *Harmonia axyridis* (Pallas) from the 5 hibernating sites (H test de Kruskal-Wallis and Student t test, < 0.05) NS = Non Significative, S = Significative; groups: II = Antibes, III = Roquebrune, IV = Alpilles, V = Courbons, VI = Tourniol

months	groups compared	H or t	X2 or tc	d of l	conclusions
january	II-III-IV	H = 2,30	X2=5,99	2	N S
february	II-III-IV-V-VI	H = 28,17	X2=9,49	4	S
	II-III-IV	H = 20,72	X2=5,99	2	S
	IV-V-VI	H = 2,28	X2=5,99	2	N S
	II-III	t = 5,28	tc =2,02	35	S
beginning of March	III-IV-V-VI	H = 13,02	X2=7,81	3	S
	IV-V-VI	H = 1,11	X2=5,99	2	N S
end of March	II-III-IV	H = 1,20	X2=5,99	2	N S

CONCLUSIONS

In *H. axyridis* dormancy is induced in late preimaginal and early imaginal life by a photoperiod shorter than 14:40 hours (Ongagna & Iperti 1994). Hibernating adults initially have enlarged fat body and a midgut generally empty of food. The ovaries of the females are poorly developed and lack follicle. In contrast the follicular tissues in the tests of the males remain active throughout hibernation.

From January the beetles are in a state of quiescence and spring emergence is dependent on the ambient temperature. The intensity of dormancy gradually decreases during winter untill the preoviposition period is 7 days. At all five hibernation sites, adult mortality was very low: less than 9%.

Thus, the hills and mountains of South Eastern France are favorable sites for overwintering of this coccinellid. The only difference among the hibernation sites was in the timing of the spring emergence, which was dependent on altitude, earliest (the end of March and the beginning of April) at Antibes, at Rocher de Roquebrune and Alpilles (<260 meters) at the end of April, and at the beginning of May at Courbons (1200 meters) and at Col de Tourniol (1180 m).

As *Harmonia axyridis* is easily reared on the eggs of *A. kuehniella* (Schanderl et al. 1988) and is able to hibernate in South Estern France should make it easy to acclimatize this species in France.

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Seasonal life cycles and the forms of dormancy in ants (Hymenoptera: Formicoidea)

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Abstract. The forms of dormancy found in ants range from simple quiescence to profound diapause. Most tropical ants are *homodynamic* and have no developmental arrests: all ontogenetic stages from egg to pupa are present in their nests throughout the year. Some of them (*quasi-heterodynamic* species) have penetrated into the regions with warm temperate climates but did not evolve real diapause. The development of their brood ceases only at temperatures below the threshold of development (consecutive dormancy) and ants overwinter in a quiescent (cold coma) state suffering from more or less strong mortality. Most temperate ants, however, are *true heterodynamic*, i.e. they possess real winter diapause (prospective dormancy). In *exogenous-heterodynamic* species diapause in larvae and queens is *facultative* and arises in direct response to falling temperatures in autumn, but diapause begins after some delay and when temperatures are still well above the threshold of development. The diapause in *endogenous-heterodynamic* species is *obligatory at a colony level* in a sense that it ensues sooner or later under any circumstances. Their intrinsic brood-rearing cycle is limited by an endogenous timer called *a sand-glass device* and is also controlled by environmental cues – temperature and photoperiod (in some species), which can only advance or delay the onset of diapause to some extent. Larval dormancy in these ants is *facultative diapause* induced by social influences of the nurse workers and temperature cues. Adult dormancy is *obligate diapause* characterized by inactive state of ovaries and also by inability of workers to maintain high growth rate and non-diapause development of larvae and normal egg production of queens. The adult and larval diapause in some endogenous-heterodynamic species is quite stable even at high temperatures and long days but in many others diapause can easily be terminated in such circumstances. In many ants, both endogenous- and exogenous-heterodynamic, the diapause larvae in the last instar continue to feed and to grow slowly and can attain significantly larger size before overwintering. The diapause completion in temperate ants is normally a result of cold reactivation, i.e. the winter exposure to low temperatures, which also leads to (1) the restoration of the colony's "spring physiology" and full capability to realize a new brood-rearing cycle, and (2) the changes of the norm of reaction to photoperiod (general loss of sensitivity in species that have photoperiodic responses) and temperature (ability to produce eggs and rear larvae without diapause at rather low temperatures that induce diapause in summer).

Seasonality, climate, temperature, photoperiod, development, diapause, exogenous, endogenous, social, control, Hymenoptera, Formicoidea, Formicidae

INTRODUCTION

Despite extensive studies of arthropod dormancy and seasonality during the last several decades, most ant specialists remained indifferent to this subject. As a result the papers specially devoted to phenology, diapause and seasonal cycle control are rather scarce in myrmecological literature; more frequently these questions are discussed only parenthetically and given less prominence than the main problem under consideration (for examples see the review of Brian 1977). In the fundamental modern treatise "The Ants" by Hölldobler & Wilson (1990) the seasonality of development is not even mentioned.

Our studies were, therefore, devoted to the elimination of this gap in ant ecophysiology and sociobiology. Since 1969 more than 70 ant species belonging to 21 genera and four subfamilies from different regions of the former USSR have been studied in our laboratory. We used two main research methods: laboratory experiments and field phenological observations. In experiments the colony fragments (more rarely the whole natural colonies) consisting of workers, queens (or a single queen in monogynous species) and the brood were used. They were kept in artificial plastic nests under different constant temperatures (or thermoperiods) and photoperiods. Our culturing methods allowed us to observe and to study in the laboratory all phases of ant annual cycle including the overwintering in a refrigerator under 3–5 °C. This research resulted in a classification of the structural diversity of ant annual cycles, revealed the primary factors of their control and led to some ideas on the possible ways of their evolution (Kipyatkov 1981, 1993, 1994, 1996, Kipyatkov & Lopatina 2002b, c).

The main purpose of this paper is to consider the types of seasonal development and the forms of dormancy found in ants in connection with the mechanisms of their control. This review is based on the results of our studies and also on data in the literature.

MAIN TERMS AND DEFINITIONS

The terms *seasonal development* and *seasonal life cycle* are traditionally used to designate the seasonal differences in the development and physiology of individuals of a species at different times of year (e.g., Danilevskii 1961). The annual cycle of development of a species is, therefore, a succession of the individual life cycles of different generations (in polyvoltine species), the whole life cycle of a single generation (in monovoltine species) or a sum of different parts of the life cycles of several successive generations (in semivoltine and perennial species). Ants are social insects and their colonies are not only perennial but usually even have unlimited life cycle i.e. are potentially immortal unless environment becomes too adverse (Bourke & Franks 1995); adult ants (especially queens) also live for several years (Hölldobler & Wilson 1990). The brood and workers in an ant colony may all belong to the same genetic generation (in monogynous species having a single queen in each colony) during several successive years (while the same mother queen is alive) or they may belong to different but overlapping generations (in polygynous species having several queens in each colony). But the seasonal life cycle of a colony has nothing in common with the differences between generations. Instead, it involves the regular seasonal changes in developmental paths, physiological states and behaviour of individuals of all generations composing a colony. This is why the seasonal life cycle of an ant colony should be better referred to as *the annual cycle of development, physiology and behaviour* (Kipyatkov 1993, 1996).

In spring ants awake from the winter dormancy and begin their routine activity, the workers start to rear larvae (if the species overwinter with brood), a queen (or queens) begins to lay eggs from which new larvae originate, the larvae grow, pupate and become new workers or alate reproductive females and males. The oviposition and brood development continue through the whole warm season until queens enter diapause and stop laying. Before the onset of winter all the eggs and young larvae develop into adults or up to a stage at which dormancy ensues and the colony moves to a overwintering place with diapause larvae or without brood. The workers also enter diapause in autumn and accumulate the nutrients in their bodies necessary for overwintering and early spring activity. Thus, each individual ant (queen, worker and even some larvae) can enter diapause and resume non-diapause activity several times in its life. This situation is unique for ants and other social insects with perennial colonies and only partly resembles extremely long perennial life cycles found in a few non-social insect species (cf. Danks 1992).

Roubaud (1922a, b, 1925) first distinguished *homodynamic species* of insects which have no diapause but only quiescence ("pseudo-diapause" of Roubaud) due simply to low temperature conditions and immediately resume their activity after the rise of temperature and *heterodynamic species* possessing true diapause ("diapause vrais" of Roubaud) that arises well in advance of the onset of adverse conditions and cannot be easily terminated by the rise of temperature. This valuable dichotomy is used for the classification of ant annual cycles of development described below. I also follow Müller (1965, 1970) in distinguishing two main forms of arrested development: *consecutive dormancy* or *quiescence* and *prospective dormancy* or *diapause*.

Ants have diverse forms of dormancy ranging from simple quiescence to profound diapause (Tab. 1). Only larvae and adults can enter diapause; embryonic (egg) diapause and pupal diapause are unknown in ants as well as in most other Hymenoptera (Danks 1987). Some authors (e.g., Tauber & Tauber 1981, Tauber et al. 1986) insisted on a narrower definition of diapause as "hormonally mediated state of low metabolic activity". However, the known cases of arrested development in arthropods range from total cessation of activity to suppressed development with less extensive effects on growth (Danks 1987). This appears especially true for ants (see below) and I therefore prefer to follow Danks (1987) in using a wider and most appropriate definition of diapause that does not require low metabolic activity and growth arrests, but only definitive suppression of development or reproduction.

Another term, *cold reactivation* (Danilevskii 1961), used in this paper needs some comments. Temperature evidently plays multiple roles during insect diapause which are not yet completely understood; moreover, the diapause-development responses are not limited to the effects of temperature and in fact can be much more complex (see Danks 1987, Hodek & Hodková 1988). In particular, the role of low temperatures in termination of diapause as well as the relevance of the term "cold reactivation" itself have been disputed by some authors (Hodek & Hodková 1988, Zaslavski 1988, Hodek 1996). Although their arguments seem to be very sound in regard to the proximate causes of the diapause termination itself, I still find it appropriate to use the term "cold reactivation" to describe the apparent effects the overwintering at cool temperatures on an ant colony, namely, the restoration of colony's "spring physiology" and full capability to realize a new brood-rearing cycle (to be detailed below). As applied to ants I employ this term in addition to commonly used Andrewartha's "diapause development" (Danks 1987) and Hodek's "diapause completion" (Hodek 1983, 1988, Hodek & Hodková 1988) because the expression "cold reactivation" helps to emphasize in the best way the restoration of colony's spring physiological state rather than simply diapause completion.

HOMODYNAMIC DEVELOPMENT

Most ant species living in the tropics and warm subtropics have homodynamic seasonal development (Kipyatkov 1993, 1996). All ontogenetic stages from egg to pupa are always present in their nests, which means that development continues without any arrests throughout the year (Tab. 1). However, significant seasonal variations in the abundance of certain brood stages and especially of the winged reproductives can usually be observed. For example, in *Cataulacus guineensis* in tropical Africa the number of the brood has two maxima – in May and in September; alates are numerous in nests from July to October and are absent during other months (Ackonor 1983). The larvae of alates of *Camponotus sericeus* in India develop from October to July and the nuptial flight takes place in September–October (Basalingappa et al. 1986, 1989). The seasonality of alate production has also been reported for *Anoplolepis longipes* in Papua New Guinea (Baker 1976) and in the Seychelles (Haines & Haines 1978), *Camponotus detritus* in the Namib desert (Curtis

Tab. 1. Description of main types of dormancy and seasonal life cycles in ants

species group	homodynamic	quasi-heterodynamic	exogenous-heterodynamic	endogenous-heterodynamic
area of occurrence	Tropics, warm temperate climates	Subtropics, regions with warm of temperate zone	subtropics, southern part of temperate zone	temperate zone, regions with boreal climates up to the subarctic; tropics and subtropics (probably)
seasonal cycle and overwintering in nature	all ontogenetic stages throughout the year, no overwintering	all ontogenetic stages remain at the onset of winter	eggs and larvae of all instars can overwinter or only diapause larvae	overwintering with diapause larvae or without brood
Adaptations to cold winters	No adaptations; quick death at temperatures below the threshold	Some adaptations exist; more or less severe mortality of brood and adults at temperatures below the threshold	Good adaptations High winter survival	Good adaptations High winter survival
Forms of winter dormancy				
in larvae	No developmental arrests or dormancy	Consecutive dormancy: *simple quiescence* at temperatures below the threshold	Prospective dormancy: *facultative diapause* induced by suboptimal (but exceeding the threshold) temperatures after some delay	Prospective dormancy: *facultative diapause* induced by temperature cues and social influences
in adults	No delays of oviposition, no forms of physiological rest	Consecutive dormancy: *simple quiescence* at temperatures below the threshold	Prospective dormancy: *facultative diapause* induced by suboptimal (but exceeding the threshold) temperatures after some delay	Prospective dormancy: *obligate diapause*, environmental cues (temperature and sometimes photoperiod) can only advance or delay its onset
Stability of diapause	–	–	*Reversible*, can easily be ended by reentering the optimal temperature range (after some delay)	*Unstable*, can easily be interrupted by above-optimum temperatures or long days (many species) *Extremely stable*, cannot be broken by high temperatures and long days (some species)
Brood-rearing cycle in constant optimal conditions (in a laboratory)	Unlimited and incessant oviposition and brood-rearing	Unlimited and incessant oviposition and brood-rearing	Unlimited and incessant oviposition and brood-rearing	Intrinsic cycle of oviposition and brood-rearing limited by an endogenous sand-glass device

1985), *Pseudomyrmex* sp. in Texas, USA (Baldridge & DeGraffenried 1988) and for many species of Neotropical army-ants (Schneirla 1977, Rettenmeyer et al. 1983). The proximate causes of this seasonality in tropical ants are unknown.

Uninterrupted homodynamic development was also observed in prolonged laboratory experiments under optimal temperatures in tropical ants *Tetraponera anthracina* (Terron 1977) and *Monomorium pharaonis* (Peacock & Baxter 1949, 1950, Peacock 1950b, Peacock et al. 1955, Petersen Braun 1975, 1977). Our experiments revealed the homodynamic type of development for three tropical species – *M. pharaonis* collected in St. Petersburg, *Pheidole sexspinosa* from Tonga Archipelago and *Tetramorium semillimum* from the Seychelles. These species were kept in the laboratory during 1.5–2 years under various ecologically feasible conditions (temperature from 18 to 25 °C, photoperiods from 10 to 16 hours of light per day) and incessant development without any sign of arrest was invariably observed.

However, when colonies of Pharaoh's ant *M. pharaonis* were kept at temperatures close to or below the threshold of development, which is about 17.7–17.8 °C (Kipyatkov & Lopatina 2002a), the mortality of brood and workers became too high and the colonies died out in a month. This finding is in good accordance with the fact that Pharaoh's ant occurs in Europe only in well-heated buildings (Berndt & Eichler 1987). Unfortunately, other tropical ants are still unexplored in this respect. It is well known, however, that true tropical insects are unable to survive long at temperatures near or below the threshold for development and especially below the cold coma point i.e in the state of quiescence (Leather et al. 1993). Thus, most homodynamic tropical ants are not preadapted to cold weather and would not survive even in warm temperate regions.

QUASI-HETERODYNAMIC DEVELOPMENT

The term *quasi-heterodynamic* can be applied to tropical ants that are adapted to exist in the regions with cold winters but unlike true heterodynamic (see below) species do not have real diapause (Kipyatkov 1996). In optimal conditions the egg-laying of their queens and the development of their brood can proceed indefinitely and cease in nature only at temperatures below the threshold of development (consecutive dormancy). The colonies overwinter in a quiescent (cold coma) state suffering from more or less strong mortality (Tab. 1). These species differ from true homodynamic ants only in this ability to survive somehow during cold winters. Several examples are described below.

The red and black imported fire ants, *Solenopsis invicta* and *S. richteri*, were accidentally introduced into the United States from South America about 60 and 80 years ago, respectively, at the port of Mobile, Alabama (Lofgren 1986). Today, the red imported fire ant is distributed throughout most of the southeastern United States and the black imported fire ant is primarily restricted to northern Alabama and Mississippi and southern Tennessee (Lofgren 1986). Thus both species now occur in the regions with relatively cold winters. In fact they are homodynamic in the Southern United States since all developmental stages occur in their nests throughout the year, although the amount of brood can be very low during mid-winter (Markin & Dillier 1971, Horton & Hays 1974, Lofgren et al. 1975). However, in the northern parts of the fire-ant range, oviposition in colonies ceases during the coldest period of the winter and most larvae and pupae disappear (Markin et al. 1974, Lofgren et al. 1975). As long as the lower threshold of larval development in *S. invicta* is about 17 °C (Porter 1988) many larvae (and also adult workers) may perish during the winter in northern populations of this species. Such winter mortality of workers is documented for *S. invicta* (e.g., Morrill 1977, Morrill et al. 1978).

The Argentine ant, *Linepithema humile*, from South America has infested many territories all over the world. The seasonal life cycle of this species studied in the South of California, USA (Markin 1970) and in the South of France (Benois 1973) appeared rather similar to that of the fire ants. Only a few larvae (mainly small) and very few eggs can be found in the nests of *I. humilis* during the winter when adults make up more than 90% of colony biomass. In summer the brood constitutes about 50% of the biomass but in October it quickly declines and reaches a minimum by December.

The primarily tropical army-ants of the genus *Neivamyrmex* in northern parts of their range exist in a temperate climate with rather cold winters. According to the observations of Schneirla (1958, 1971) in autumn when nights grow cooler these nocturnal ants cease foraging. Then the lack of food forces the queen to stop laying, the workers destroy the remaining brood and the colony, comprising only adult ants, passes the winter in a shelter. In spring when temperatures rise the queen starts laying and the colony gradually restores the periodicity of brood-rearing and nomadic behaviour typical of the summer season (Schneirla 1963, 1971). Schneirla postulated the direct influence of low temperatures on the development of these ants. However, this statement has never been tested experimentally.

We have studied the quasi-heterodynamic development in three species of myrmicine ants. *Pheidole pallidula* occurs in South Europe, the Caucasus and Middle Asia (Dlussky 1981); the range of *P. fervida* includes South-East Asia, Japan, Southern Kurils and the South of Primorie (Kipyatkov & Lopatina 1987, Kupyanskaya 1990). In Primorie *P. fervida* is likely to have persisted from the Tertiary when the climate was much warmer (Kupyanskaya 1990).

In experiments on both *Pheidole* species (Kipyatkov 1993, 1996) the queens laid eggs and the larvae continued to develop and pupate uninterruptedly under any temperature above the lower developmental threshold. Thus, any form of diapause is absent in these ants. We have observed incessant and unlimited development in their colonies at optimal temperatures of 25–28 °C during more than two years. In *P. pallidula* from Turkmenistan oviposition and larval development did not cease at 20 °C. After temperature decreased below the developmental threshold, which is about 18 °C in this species (Kipyatkov & Lopatina 2002a), the queens still continued to lay but the eggs did not develop, prepupae and pupae began to perish and all the brood gradually died out. The overwintering of this species without brood was confirmed by our field studies in Turkmenistan and by the observations of Passera (1977) in Southern France.

P. fervida, appeared to be better adapted to the rather severe winters of the Southern Primorie because its brood perished only partially during artificial overwintering. After temperature decreased up to 10–12 °C in an experiment the workers began to dismember and discard the pupae and prepupae and gradually destroyed all of them. The ants overwintered, therefore, with eggs and larvae of all instars. However, some proportion of eggs and young larvae died out during the artificial overwintering, whereas older larvae overwintered successfully (Kipyatkov & Lopatina 1987).

In *Monomorium kusnezovi* from Turkmenistan (Kipyatkov 1996) the growth and pupation of larvae continued without delays at all temperatures above the threshold of development (between 20 and 21.5 °C for eggs, larvae and prepupae – Kipyatkov & Lopatina 2002a). Thus, the larvae of this species have no diapause. At 20 °C and below the larvae ceased to grow but the queens continued to lay eggs. Therefore, the ant colonies contained eggs and larvae of all instars before the artificial overwintering. Most eggs died during overwintering but larvae survived more successfully. The overwintering of *M. kusnezovi* larvae was also confirmed by our field observations in Turkmenistan (Kipyatkov 1996).

TRUE HETERODYNAMIC DEVELOPMENT

Most temperate ants are true heterodynamic, i.e. they have a period of prospective dormancy (winter diapause) in their annual life cycle. However, heterodynamic development has been found in some tropical species as well. For example, all five species of *Rhytidoponera impressa* group widespread in the forests of East Australia were found to have a distinct seasonality of development: only small and medium size larvae and very rarely some eggs but no large larvae and pupae are present in their nests during the winter months, this seasonality being clear-cut both in the tropical and subtropical regions of Australia (Ward 1981). *Prenolepis imparis* in the northern part of Florida, USA (Tschinkel 1987) and *Polyrhachis vicina* in the warm subtropics of China (Chen & Tang 1989, 1992) are also heterodynamic. As long as seasonality of the environment is usually quite apparent in the tropics, heterodynamic development with true diapause might be very common in tropical ants. Unfortunately, the data are still very scarce. Recent investigations give ever more evidence that various forms of dormancy and diapause are widespread phenomena in tropical and subtropical insects but the factors controlling dormancy in these species are as yet insufficiently known (Denlinger 1986, Danks 1987). It is worth emphasizing that heterodynamic development can serve as a preadaptation for survival during cold winters and facilitate the expansion of some tropical ants to temperate regions (Kipyatkov 1993, 1996).

In a pioneering study of life history evolution in social insects Oster & Wilson (1978) primarily concentrated on the scale and timing of the allocation of resources between worker and sexual production. They distinguished three main stages in a colony's life cycle: *foundation stage* when the solitary queen attempts to start its colony, *ergonomic stage* in which the colony grows by producing all-worker broods for a number of years, and *reproductive stage* in wich the colony each year produces a mixture of workers and sexuals. For the perennial species, such as ants, Oster & Wilson (1978) predicted so-called "*bang-bang*" *strategy* which maximizes colony's fitness (sexual production) by alternation ergonomic and reproductive phases within each year. The ergonomic phase within each season should be as long as possible so that more workers are available to raise the largest number of sexuals during the second part of the year. Such seasonal switches to sexual production resulting in clear oscillations in numbers of worker present in a colony were indeed observed in several species, such as *Solenopsis invicta* in the USA (Tschinkel 1993).

However, the perennial colonies also have to invest in workers to promote winter survival and subsequent reproduction. Considering this constraint Oster & Wilson (1978) predicted that the switch to producing sexuals should occur later within a season as the colony overwintering survival rise. Since then little attention has been paid to the role of seasonality in life history evolution in ants (e.g., Bourke & Franks 1995). Recently, the thorough analysis of literature and own data collected during many years of field work allowed Kipyatkov (1996) to conclude that most temperate ants evidently differ in seasonal timing of worker and sexual production from the predictions of Oster and Wilson. First, most species raise their alate reproductives not in late summer after the worker brood is already produced, but quite the reverse – just after the overwintering. In some of them sexuals originate from the first egg portion laid by queens in early spring. This group comprises species belonging to the tribe Formicini (genera *Alloformica*, *Cataglyphis*, *Formica* and *Proformica*) and the genera *Dolichoderus* and *Pogonomyrmex* (Kipyatkov 1996). Another, much larger group consists of all other temperate species in which alates develop from the overwintered larvae (Kipyatkov 1996). Anyhow, the rearing of sexuals always precedes the period of worker production in an annual cycle of most temperate ant species. The second departure from the predictions of Oster and Wilson is that the production of sexuals is always accompanied by rearing of workers which can emerge even in greater numbers than winged reproductives (Kipyatkov 1996). It means that a complete switch from worker to alate production does not in fact occur.

Thus, most temperate ants use *the strategy of preceding production of sexuals* in their annual cycle (Kipyatkov 1996). This strategy demands that the colony's annual cycle should be organized in a way to maximize the quantity of diapause larvae and new workers produced by the end of each brood-rearing season; these workers will facilitate colony's winter survival and will rear alate females and males from overwintered larvae or from eggs next spring. For this purpose the brood-rearing should start in spring as early as possible and continue as long as possible. At the same time the brood stages and adults present in the nest by the beginning of winter should be capable of overwintering. To resolve this problem the temperate ants should evolve appropriate forms of winter dormancy and efficient mechanisms controlling its onset and completion at the proper time (Kipyatkov 1993, 1996).

Temperate ants use two main *seasonal strategies of brood-rearing* (Kipyatkov 1996, Kipyatkov & Lopatina 1995, 1996a, b). The most widespread is *the strategy of prolonged brood-rearing* distinguished by delaying development of a large proportion of larvae (so-called *slow brood*) which continue to grow in autumn, overwinter in diapause and pupate during the next summer; thus, only some larvae develop from egg to pupa within the same summer season without overwintering (so-called *rapid brood*). The strategy of prolonged brood-rearing has several evident advantages important for adaptation to temperate and boreal climates (Kipyatkov 1993, 1996): (1) the larvae can be reared from early spring up to late autumn thus utilizing the whole warm period of a year; (2) the quantity of rapid brood can be changed to adapt to long-term and short-term climatic

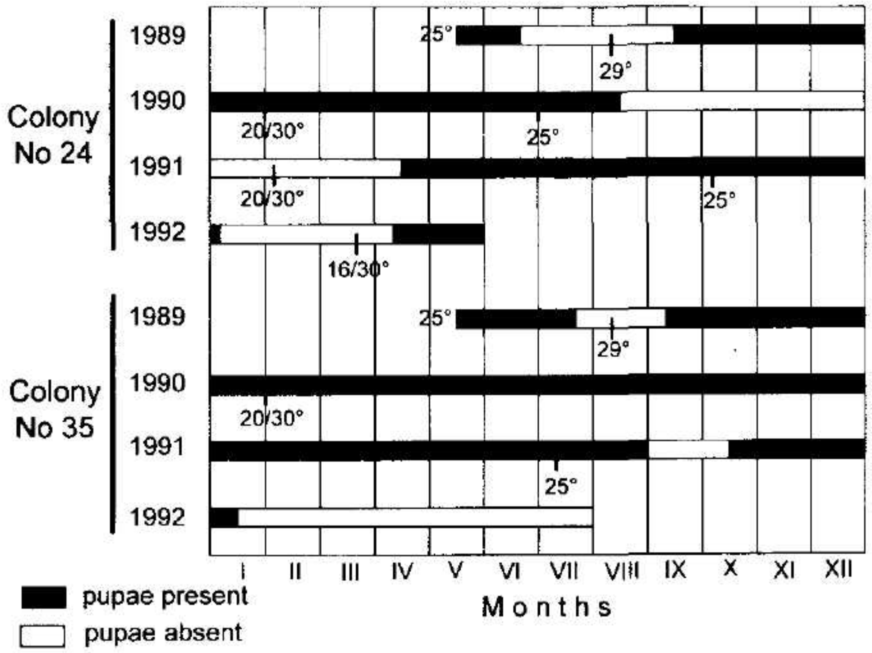

Fig. 1. Repeated induction and termination of larval diapause in two laboratory colonies of *Tapinoma karavaievi* collected in summer 1989 in Turkmenistan as a result of successive changes of temperature regimes during a period of three years. The absence of pupae in a colony indicates that larvae are in diapause.

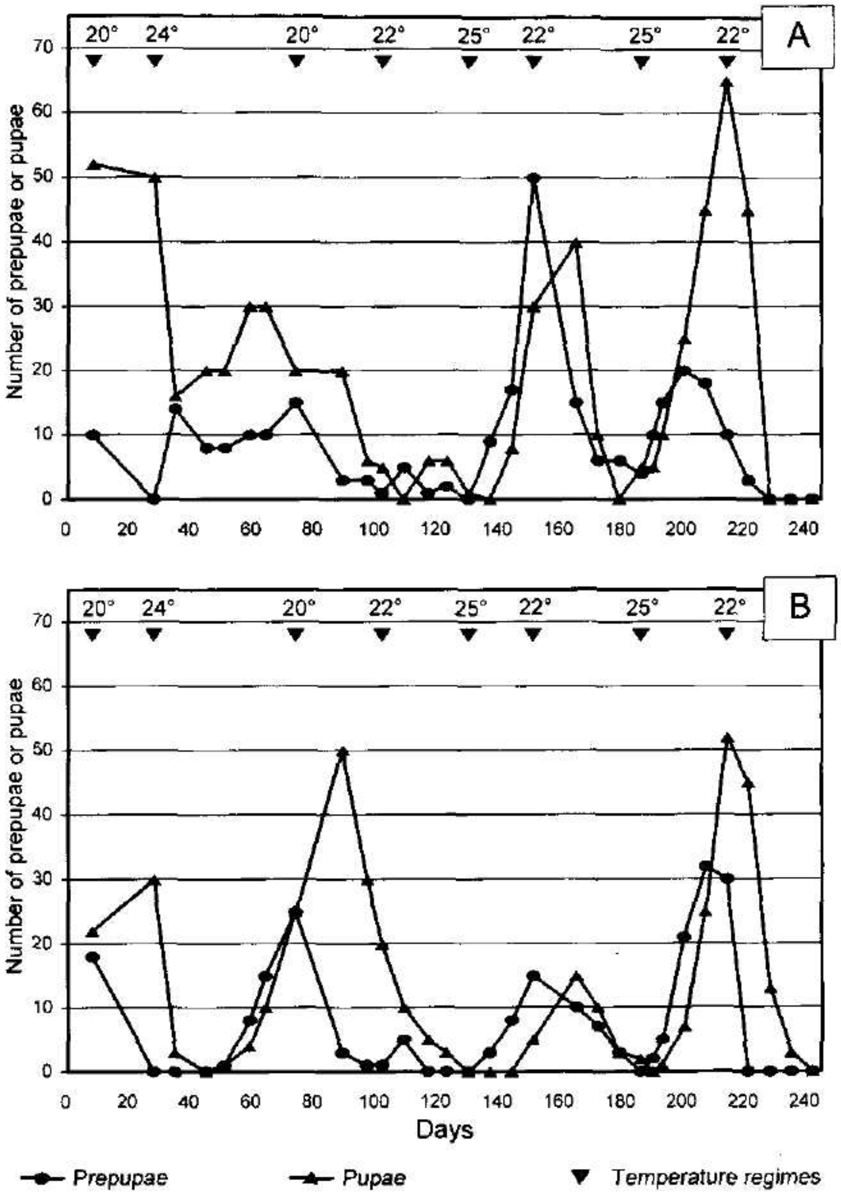

Fig. 2. Repeated induction and termination of larval diapause in two laboratory colonies (A and B) of *Tetramorium jacoti* from South Primorie (near Vladivostok) by successive alterations of temperature. Start of experiment on 17 September. The numbers of prepupae and pupae present in a colony at each census date are depicted. Since the prepupal stage lasts only several days, the absence of prepupae in a colony is a good evidence that larvae do not pupate.

variations and to the duration of the warm season; (3) the development of larvae can be extended to two or even three summer seasons.

Two *structural types* of annual cycles have been distinguished among heterodynamic species with prolonged brood-rearing (Kipyatkov 1993, 1996). In ***Aphaenogaster* type** the larvae enter diapause at the end of summer but the queens have no diapause and do not cease laying until the late autumn; therefore, not only diapause larvae but also eggs and young larvae overwinter and survive, at least partially, during the winter (Kipyatkov & Lopatina 1990). Ants with this type of cycle are apparently restricted to the subtropics and the southernmost regions of the temperate zone. It was discovered in all hitherto studied species of *Aphaenogaster* (Kipyatkov & Lopatina 1990) and in a few species of *Leptothorax*, *Messor*, *Monomorium*, *Polyrhachis*, *Tapinoma* and *Temnothorax* (Kipyatkov 1993, 1996).

Most species with prolonged brood-rearing have the second structural type of annual cycle – ***Myrmica* type**. They all have winter diapause both in larvae and adults and overwinter without eggs but only with diapause larvae of one or several instars depending on species (Kipyatkov 1993, 1996). According to the stages in which larvae can enter diapause five species groups have been distinguished (Kipyatkov 1996): (1) species with diapause in early (1–3) instars (*Lepisiota*, *Plagiolepis*, *Tapinoma*, some *Camponotus*; full number of instars – 5), (2) species with diapause in middle (2–4) instars (*Camponotus s. str.*), (3) species with diapause in the two last (3–4) instars (*Harpagoxenus*, *Leptothorax* s. str., *Messor*), (4) species with diapause in a final (usually the third) instar (*Diplorhoptrum*, *Leptanilla*, *Monomorium*, *Myrmica*, *Tetramorium*), (5) species with dia-

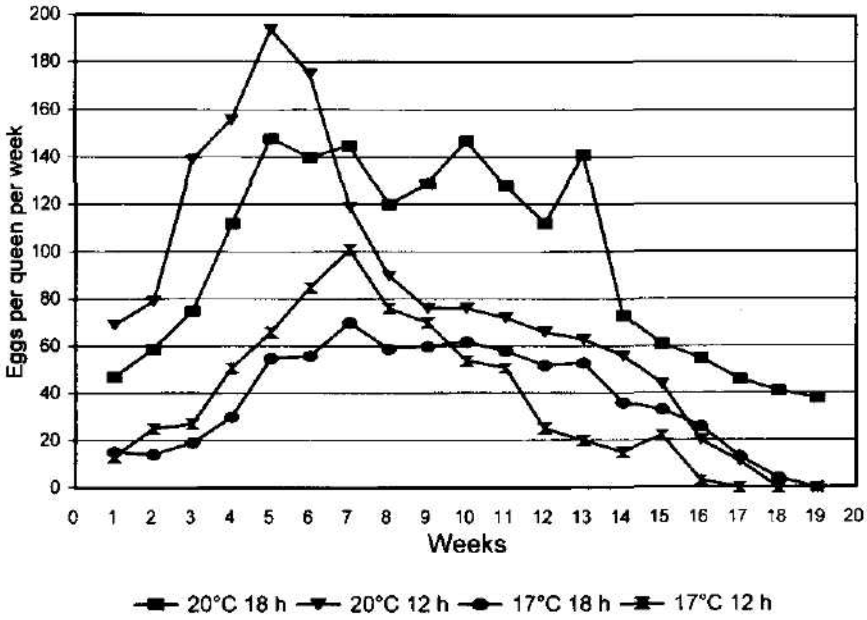

Fig. 3. Internally limited intrinsic cycle of oviposition in *Myrmica rubra* queens in cultures collected in spring in Belgorod region and kept under two temperatures and two photoperiods (according to the data of Kipyatkov 1979). Start of experiment on 17 May. Each line – the average value for 4 queens in separate cultures. Evidently, short days and lower temperature decreased the egg production and advanced the onset of diapause in queens.

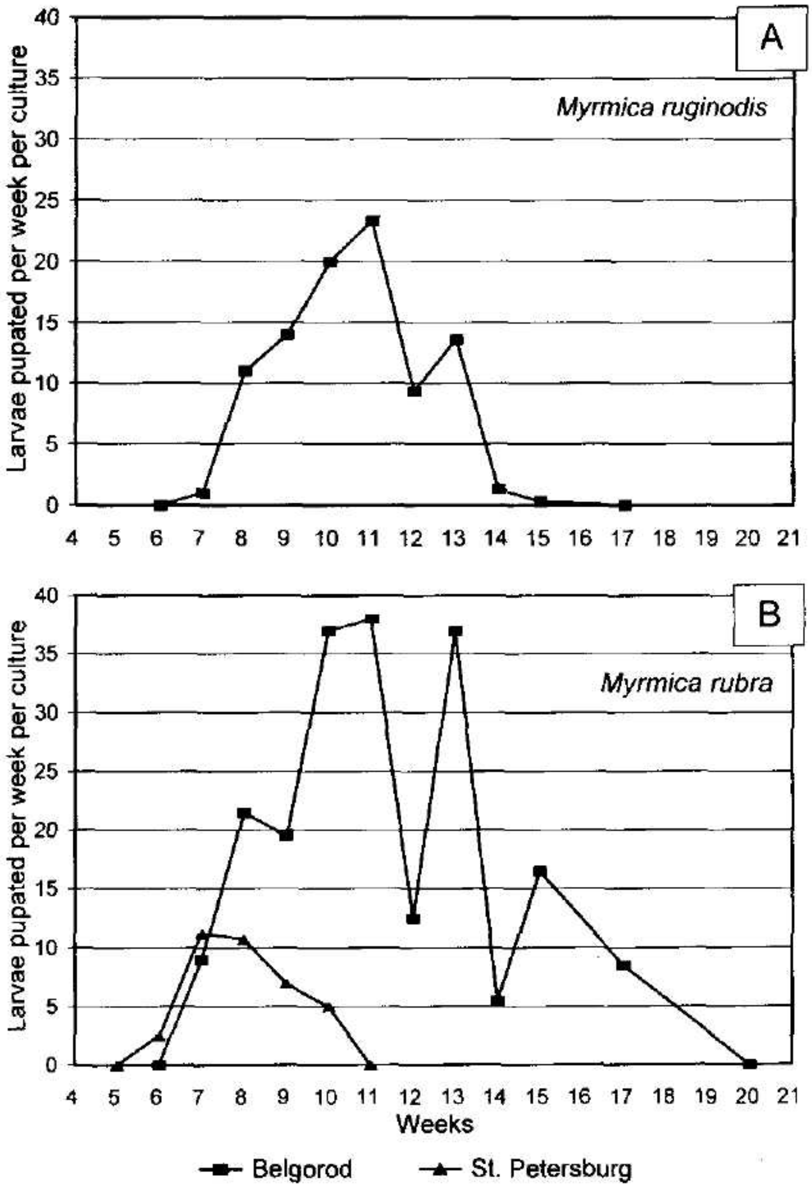

Fig. 4. Specific and geographic differences in the length of the intrinsic seasonal cycle of rapid brood production in *Myrmica ruginodis* (A) and *Myrmica rubra* (B) (according to the data of Kipyatkov & Lopatina 1997a). Ants were collected in early spring in Belgorod and St. Petersburg regions and cultured under long days (20 h) and 20 °C. Start of experiments – 13 April (Belgorod), 2 June (St. Petersburg). Each line – the average value for 4 experimental cultures. The cultures of *M. rubra* had significantly longer period of pupation and produced more rapid brood pupae than *M. ruginodis* cultures. *M. rubra* cultures from northern population (St. Petersburg) had much shorter cycle of rapid brood-rearing and produced significantly less pupae in comparison with cultures from southern population (Belgorod). *M. ruginodis* cultures from St. Petersburg did not produce any rapid brood at all.

pause in all instars (*Crematogaster*, *Lasius*, *Paratrechina*, s.g. *Tanaemyrmex* of the g. *Camponotus*; full number of instars – 5–6).

The strategy of concentrated brood-rearing is employed by ant species with another structural type of annual cycles which I call ***Formica* type** (Kipyatkov 1993, 1996). The development of all brood stages is restricted to the warm season in these ants. Only queens (and also workers) are able to diapause. Larvae have no dormancy and all finish their development during the summer, all new workers emerge from pupae until autumn cold weather and ants overwinter, therefore, entirely without brood. According to our observations and published data this strategy is characteristic for all genera of the tribe Formicini (*Alloformica*, *Cataglyphis*, *Formica*, *Proformica*) and for some species of the genera *Dolichoderus*, *Pogonomyrmex*, *Ponera* and *Prenolepis* (Kipyatkov 1993, 1996).

The onset of diapause in queens is a central point in the cycles of *Formica* type because it determines the moment after which new eggs do not appear, the brood gradually vanishes and the ants begin to prepare for overwintering. Queen diapause should not occur too early because it would not allow ants to use a part of the warm season for brood-rearing. At the same time if diapause ensues too late many larvae and pupae would not manage to finish their development and would perish due to low temperature. Evidently, the strategy of concentrated brood-rearing is only appropriate for temperate and boreal ants in combination with very fast brood development, allowing them to rear sexuals and new workers from eggs during a short warm season. In fact among temperate ants *Formica* species have the shortest developmental times and their development is more temperature dependent, which allows *Formica* workers to rear the brood much faster at higher temperatures (Kipyatkov & Lopatina 2002a).

Among ants inhabiting the temperate zone and adapted to cold winters two main groups can be distinguished according to the nature of dormancy and the type of seasonal cycle control: *exogenous-heterodynamic* and *endogenous-heterodynamic* (Kipyatkov 1993, 1996).

EXOGENOUS-HETERODYNAMIC SPECIES

In ants belonging to this group winter diapause in larvae and queens is *facultative* and arises in direct response to suboptimal temperatures in the autumn, but unlike simple quiescence in quasi-heterodynamic species this diapause begins when temperatures are still well above the threshold of development. Another important property is that the diapause ensues not immediately following the temperature fall but after some delay and is reversible, i.e. may be ended by reentering the optimal temperature range, also after a delay (Tab. 1).

We have found diapause of this kind in several species of the genera *Diplorhoptrum*, *Messor*, *Monomorium*, *Tapinoma* and *Tetramorium* which are limited in their distribution to southern regions of the Palaearctic region, i.e. they live in rather warm temperate climates (Kipyatkov 1993, 1996, Kipyatkov & Lopatina 2002b). These species are also remarkable by their ability for continuous and unlimited development under optimal temperatures, behaving as true homodynamic species in these circumstances. In our experiments several colonies of these species were kept at temperatures above 25 °C or under daily thermoperiods of 20/30 °C for more than two years and during the whole period queens continued to lay eggs, larvae emerged from eggs, grew and pupated without any delay or any changes for the worse in colony viability (Kipyatkov 1993, 1996, Kipyatkov & Lopatina 2002b).

At the same time, at suboptimal temperatures, i.e. below 23–25 °C but well above the lower threshold, development ceased after a short period. If temperatures rise after that, development will soon recommence, but it may be blocked again by the fall of temperature and then be resumed in response to a new temperature increase. We succeeded in repeating such alterations with the same ant colonies several times with similar results (Kipyatkov & Lopatina 2002b). Three examples are given below.

When summer colonies of *Tapinoma karavaievi* from Turkmenistan were kept at 28–30 °C or daily thermoperiod of 20/30 °C they displayed continuous development for months, but at 25 °C, i.e. well above the threshold of development, which is about 20 °C (Kipyatkov & Lopatina 2002a), the larvae ceased to pupate in 1–2 months and then resumed development only after the restoration of optimal temperature conditions, not immediately but after a delay of a month or more; these successive changes could be repeated over and over again (Fig. 1). Since this polygynous species has an annual cycle of the *Aphaenogaster* type, queens never stop laying except at too low temperatures and, thus, eggs are always present among the brood. Another Turkmenian species, *Monomorium ruzskyi*, has a lower threshold for larval development of 21.8 °C (Kipyatkov & Lopatina 2002a), but its larvae ceased to pupate in summer at 23–25 °C whereas under 27–28 °C or a thermoperiod of 16/30 °C the new pupae appeared in colonies for many months. A third example is the repeated induction and termination of larval diapause produced in two colonies of *Tetramorium jacoti* from South Primorie (near Vladivostok) by successive alterations of temperature (Fig. 2).

Another important feature of exogenous-heterodynamic species is the distinct change of their norm of reaction to temperature during overwintering as a result of cold reactivation. In spring oviposition and development begins in their colonies at threshold temperatures as a result of the

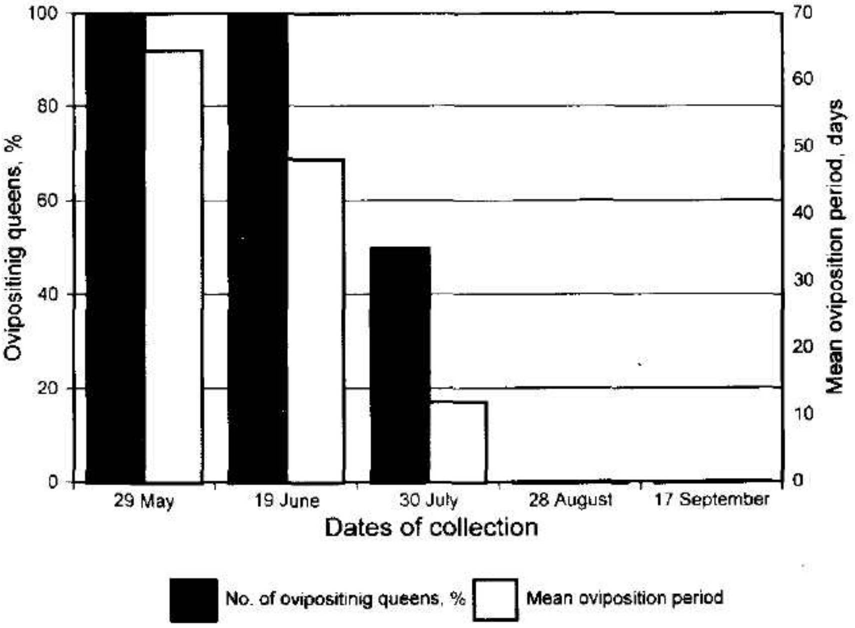

Fig. 5. Seasonal changes of intrinsically limited oviposition period in queens of *Formica aquilonia* from St. Petersburg region (according to the data of Kipyatkov & Shenderova 1989). Samples of queens and workers were collected from natural nests on five dates during May–September (from 4 to 14 queens per date) and cultured in laboratory at 25 °C and long days (20 h) until the queens stopped egg-laying. The later in the season samples were collected, the lower was the percentage of queens still laying eggs after the collection and the shorter was the mean length of their oviposition period.

absence of diapause. After natural overwintering or after exposure in a refrigerator to 3–5 °C during 2–3 months the development and pupation of larvae recommenced and proceeded for a long period at 20 °C and even at 18 °C (in some *Tetramorium*) in all species studied (Kipyatkov 1993, Kipyatkov & Lopatina 2002b). This difference in the norm of reaction to temperature, which can be easily revealed in experiments, is another indication of the existence of diapause in exogenous-heterodynamic species.

ENDOGENOUS-HETERODYNAMIC SPECIES

Most ants inhabiting the temperate zone and all northern species belong to this group. Their diapause is *obligatory at a colony level*, i.e. it is mostly due to factors internal for the colony and no external conditions can prevent the definitive cessation of oviposition and development. Even at long days and optimal temperatures, including the daily thermoperiods which are the most favourable temperature conditions for ants (Lopatina & Kipyatkov 1993, 1997), queen egg-laying capacity and worker ability to rear larvae without diapause tend to decline step-by-step in colonies of these species until oviposition and larval development stop and diapause ensues sooner or later as a result of an endogenous timer effect (Tab. 1). This timer mechanism, internal for the colony, was called *sand-glass device* to depict the gradual loss of colony's capability to produce eggs and to rear larvae without diapause (see Kipyatkov 1993, 1996, Kipyatkov & Lopatina 2002c for details).

Thus, a colony of an endogenous-heterodynamic species has an internally limited (by a sand-glass device) *intrinsic seasonal cycle of brood-rearing*. Such an endogenous physiological cycle in constant laboratory conditions was first observed in *Myrmica* by Brian for worker (1953) and queen (Brian & Hibble 1964, Brian & Kelly 1967) oviposition, and then for rapid brood production (Brian 1957, 1962, 1963). Similar results were also obtained for *Camponotus herculeanus* and *C. ligniperda* (Hölldobler 1961), several *Leptothorax* species (Cagniant 1968, Plateaux 1970, 1986, Espadaler et al. 1983, 1984), *Plagiolepis pygmaea* (Passera 1969) and *Cataglyphis cursor* (Cagniant 1979, 1980).

In our experiments internally restricted cycles of queen oviposition and/or larval development in constant laboratory conditions were found in more than 60 species of the genera *Aphaenogaster*, *Camponotus*, *Cataglyphis*, *Crematogaster*, *Formica*, *Harpagoxenus*, *Lasius*, *Lepisiota*, *Leptothorax*, *Manica*, *Myrmica*, *Plagiolepis*, *Ponera*, *Proformica* and *Tapinoma* (Kipyatkov & Shenderova 1990, Kipyatkov 1993, 1994, 1996, Kipyatkov & Lopatina 1993, 2002c, Lopatina & Kipyatkov 1990, 1993). It was then found that the intrinsic length of colony's annual cycle of brood-rearing differed not only between close species but also between geographical populations of the same species, which reflects their adaptations to local climate conditions (Kipyatkov & Lopatina 1997a,b). Examples are shown in Figs 3–6.

The best evidence for the endogenous and obligatory nature of colony diapause was provided by experiments with free choice by ants of the preferred temperature. In the first one (Kipyatkov & Shenderova 1986) two small colonies of *Formica polyctena* were kept from early spring in nests with a horizontal temperature gradient from 5 to 40 °C in which ants were permitted to make a free choice. A normal seasonal cycle of queen oviposition and larval development was observed in both colonies, during which ants with brood concentrated in parts of the nests with temperatures of 20–30 °C. In August queens stopped laying and ants began to move gradually to the cooler parts of the nests, finishing the brood-rearing process. The length of the brood-rearing cycle in experimental colonies appeared to be just the same as in nature as well as in colonies simultaneously maintained in the laboratory at constant temperature of 25 °C (Kipyatkov & Shenderova 1986). Thus, the seasonal cycle of queen oviposition is completely limited in this species by some internal

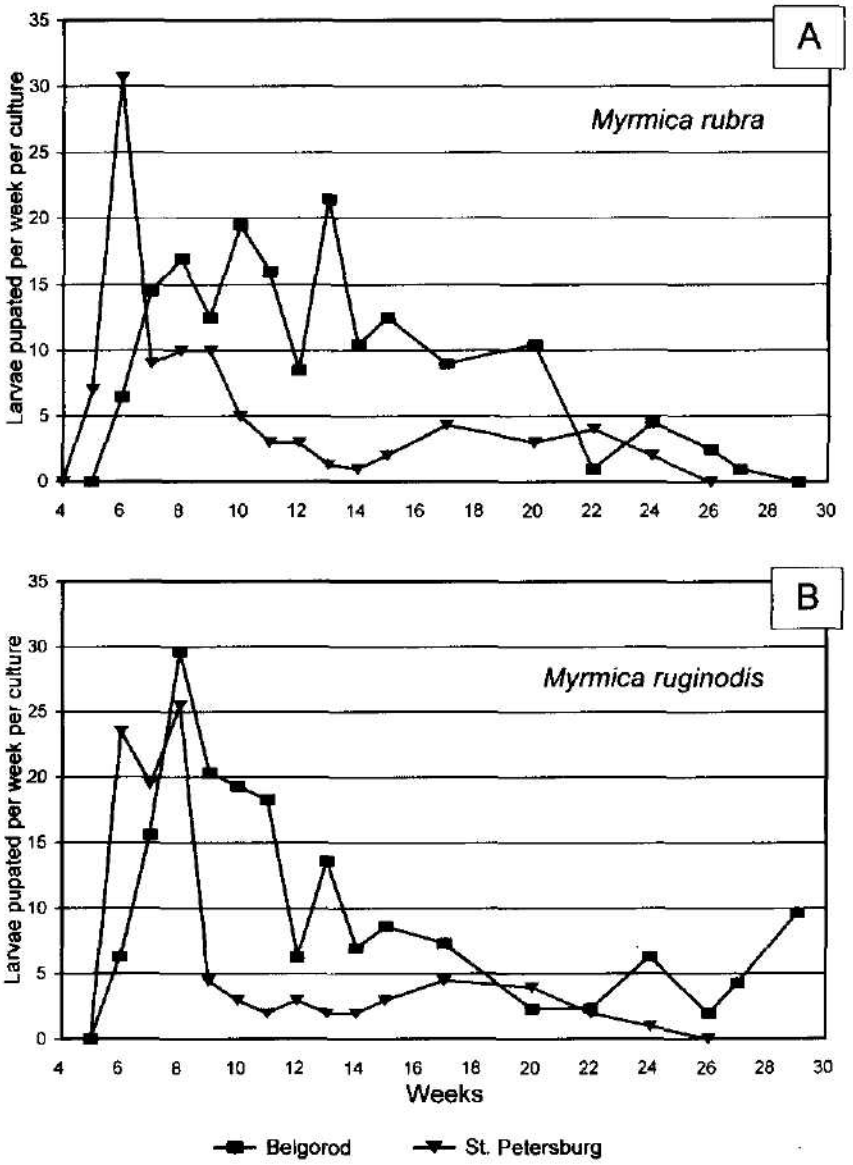

Fig. 6. Extremely prolonged production of rapid brood pupae in *Myrmica rubra* (A) and *Myrmica ruginodis* (B) cultures collected in spring in Belgorod and St. Petersburg regions and maintained under long days (20 h) and above-optimum temperature 25 °C (according to the data of Kipyatkov & Lopatina 1997a). Start of experiments – 13 April (Belgorod), 2 June (St. Petersburg). Each line – the average value for 4 experimental cultures. Even under such high temperature that strongly provoked development and pupation of larvae ant cultures from northern population (St. Petersburg) had shorter cycle of rapid brood-rearing and produced less pupae in comparison with cultures from southern population (Belgorod).

factors and cannot be extended even in favourable conditions. Similar results were later obtained for several endogenous-heterodynamic species in our prolonged experiments in nests with horizontal temperature gradients (Kipyatkov 1994, 1996).

Another confirmation for the endogenous nature of diapause control came from the observations of the *spontaneous rhythms of oviposition and development* in colonies of many ant species maintained under constant laboratory conditions for a long time: the egg-laying of queens and the development of larvae first ended, and then resumed after longer or shorter intervals, and these periods of direct development and of diapause could be repeated. Such a rhythm was first described by Hölldobler (1961) in *C. herculeanus* and *C. ligniperda*. During inactive periods of the cycle these ants formed dense aggregations in the nest together with larvae in diapause, which were fed only a little at that time, and the workers of *C. herculeanus* even closed the nest entrance then with a plug made of litter. According to the observations of Plateaux (1970) in *L. nylanderi* development in the overwintered colonies at 24–25 °C proceeded during 90–100 days and then the obligatory period of rest ensued and lasted for not less than another 100 days; after this diapause stage development could restart.

In our long-term experiments the spontaneous rhythms of oviposition and development were found in all endogenous-heterodynamic species that we studied, namely in the genera *Aphaenogaster*, *Camponotus*, *Cataglyphis*, *Crematogaster*, *Formica*, *Lasius*, *Lepisiota*, *Leptothorax*, *Myrmica* and *Plagiolepis*. In diapause ant colonies kept under conditions identical to those in which the diapause has ensued a new developmental cycle could begin after a few weeks or after several months, and sometimes after almost a year. Oviposition and pupation continued for some time, but then a gradual decline was observed, and finally development became arrested again (Kipyatkov 1993, 1994, 1996). This phenomenon was most thoroughly explored in the red wood ants *Formica aquilonia* and *F. polyctena*: the data for several dozens of experimental cultures of each species maintained at various constant temperatures and photoperiods for 1–5 years were obtained and analysed (Kipyatkov & Shenderova 1989, 1990). In nests with horizontal temperature gradients we observed even more distinct spontaneous rhythms of oviposition and development which were closely associated with changes in the thermopreferendum: during periods of direct development ants kept their brood in chambers with sufficiently high temperature, and during periods of diapause in cool chambers (Kipyatkov 1993, 1994, 1996).

There was considerable variation in the duration of periods of direct development and diapause in different experimental colonies and within the same colony. Furthermore, there was no coordination with the natural change of seasons. All this clearly indicates the endogenous nature of observed rhythms and the absence of external synchronizers (Kipyatkov 1993, 1994). This situation seems to be very similar to that found in some non-social insects which diapause as adults in which alternations of ovipositional arrest and resumption of oviposition can also be repeated in constant conditions (Hodek 1979, 1983). After analysing the available data Hodek (1998) came to the conclusion that this rhythmic alternation in the bug *Aelia acuminata* is endogenous and may be governed by internal timer(s), which is clearly analogous to my idea of a sand-glass device in ants. It is premature to discuss possible physiological mechanisms underlying these spontaneous rhythms. It should only be added that the available data distinctly demonstrate a rather complex nature of the sand-glass device in ants, which includes not only some unknown physiological mechanisms operating inside the bodies of individual ants but also a set of intricate social mechanisms functioning among individuals in a colony which control the onset and the end of diapause (Kipyatkov 1981, 1996, Kipyatkov et al. 1997a,b, Kipyatkov & Lopatina 1999). The latter mechanisms have so far been much better studied and understood (see below).

It should be emphasized, however, that in most endogenous-heterodynamic ants, especially in species occurring in the northern regions of Palaearctic, after the spontaneous completion of diapause in the laboratory the reproduction and development are never as perfect as after normal overwintering at low temperatures: the productivity of queens is low, not all overwintered larvae pupate and there is no rapid brood at all. Such a peculiarity of spontaneous resumption of development was first recorded by Plateaux (1970) in *L. nylanderi*. In our experiments we observed this phenomenon in all northern species studied. After each brood-rearing cycle under constant conditions the indices of productivity decrease steadily, the number of pupae produced and the number of ants in a culture gradually declines, their viability diminishes and finally they all die. In most prolonged experiments with red wood ants we sometimes added pupae from other colonies in order to maintain the number of workers in experimental cultures and prevent their dying out (Kipyatkov & Shenderova 1990). In fact, all endogenous-heterodynamic species require not only diapause completion but exactly cold reactivation, i.e. the winter exposure to low temperatures, to adequately restore their ability for productive brood-rearing (Kipyatkov 1994, 1996, Kipyatkov & Lopatina 2002c).

The necessity of winter chilling for diapause completion in ants was first revealed by Delage (1968) for queen diapause in *Messor capitatus* and by Cagniant (1968) for larval diapause in *Leptothorax monjanzei*. Then Passera (1969) discovered that when the workers of *P. pygmaea* kept without a queen at optimal temperature stopped laying after a long period of oviposition they could be provoked to renew egg-laying by keeping them at 10 °C for no less than 15 days. Plateaux (1970, 1971) showed a 3–4 months exposure of *L. nylanderi* colonies to cold during autumn and winter to be crucial for the resumption of full development in spring. In some ants after a nuptial flight the inseminated queens establish new nests at the end of summer but start egg-laying only in spring and need winter chilling for this (Benois 1972, Plateaux 1970). Finally, the overwintering at cool temperature was shown to be obligate for the production of alate sexuals, especially females, in numerous species of temperate ants (Wesson 1940, Chauvin 1947, Brian 1955, Otto 1962, Passera 1969, Plateaux 1970, 1971, Buschinger 1973, Schmidt 1974, Cagniant 1988). Brian (1955) first demonstrated experimentally that overwintering at low temperatures was crucial for workers of *Myrmica ruginodis* to gain the ability to terminate diapause in autumn larvae and for large diapause larvae to acquire the potency to develop into reproductive females. He called this process "vernalisation".

In our experiments such an essential role of cold reactivation was revealed for all endogenous-heterodynamic species studied (Kipyatkov 1993, 1996, Kipyatkov & Lopatina 2002c). According to our data a period of 1–4 months (depending on species) of exposure to 3–5 °C is required for full reactivation. After such a treatment oviposition and development begin even at short days and 17–20 °C, i.e. in circumstances that cause quick diapause onset in the same colonies in summer (see below). Thus, besides the completion of diapause, which may happen spontaneously or as a result of the influence of long days, the apparent effects of cold reactivation, unachievable for temperate ants without winter cooling, include: (1) the restoration of the colony's "spring physiology" and full capability to realize a new brood-rearing cycle (normal queen fecundity, potency of some larvae to develop into female reproductives, ability of workers to rear overwintered and rapid brood larvae without diapause and to produce alate sexuals), and (2) the changes of the norm of reaction to photoperiod (general loss of sensitivity in species that have photoperiodic responses – see below) and temperature (ability to produce eggs and rear larvae without diapause for a long period at rather low temperatures that induce diapause in summer). One could say that as a result of cold reactivation the ant colony's "sand-glass" turns over (Kipyatkov 1993, 1996).

During the summer season the gradual decrease of a colony's capability to produce new eggs and to rear larvae without diapause and the increase of the bias for diapause occur as a result of the endogenous physiological and social processes, as though the sand in the ants' "sand-glass" pours little by little out the upper reservoir to the lower one. Also, the photoperiodic sensitivity of a colony appears and the reaction to temperature distinctly changes due to this process. As a result, in late summer lower temperatures and shorter days (only in some species) advance the onset of diapause, thus curtailing the period of oviposition and development. Such effects of external conditions were found in our experiments in all species studied (Kipyatkov 1974a, 1977a, 1979, 1981, 1993, 1996, Kipyatkov & Shenderova 1989, 1991, Kipyatkov & Lopatina 1990, 1993, 2002c, Lopatina & Kipyatkov 1993). Thus, the duration of a colony's annual cycle of brood-rearing in nature is controlled both by an endogenous timer (sand-glass device) and by exogenous environmental cues – temperature and photoperiod (in some species), which adjust the date of diapause onset to the climatic characteristics of a given year (Kipyatkov 1993, 1996, Kipyatkov & Lopatina 2002c).

Temperature control of diapause is really universal in ants. In all species tested in our experiments higher temperatures delayed and lower temperatures advanced the onset of diapause both in larvae and adults (Kipyatkov 1993, 1996, Kipyatkov & Lopatina 2002b,c). On the contrary, *photoperiodic control of diapause* is unexpectedly uncommon among ants. The photoperiodic responses in these insects were revealed for the first time in *M. rubra* and *M. ruginodis* (Kipyatkov 1972, 1974a). It has been shown that diapause arose sooner in larvae and queens the shorter was the day-length in the interval from 16 to 13 h characteristic for the study region in July–September (Kipyatkov 1974a, 1977a, 1979). When ant colonies in the autumn state were subjected to day-lengths of 15 h, diapause ended both in queens and larvae (Kipyatkov 1977b). Subsequently the existence of photoperiodic responses in *M. rubra* was confirmed by Hand (1983) and Brian (1986).

Nevertheless, the following extensive studies demonstrated that only some ants besides *Myrmica* used day-length as an environmental cue controlling oviposition, development and diapause onset. The diapause induction was found to depend on photoperiods only in *Aphaenogaster sinensis* (Kipyatkov & Lopatina 1990) and *Lepisiota semenovi* (Kipyatkov & Lopatina 2002c). In addition in *A. sinensis*, *Camponotus herculeanus*, *Leptothorax acervorum* and *Manica rubida* we have observed higher incidence of diapause in larvae at short days compared with larvae in similar cultures at long days (Kipyatkov 1996). The genus *Myrmica* thus represents a rather curious exception among temperate ants since all its species studied so far possess clear-cut photoperiodic responses controlling the induction and termination of diapause (Kipyatkov 1972, 1974a, 1993, 1996, Kipyatkov & Lopatina, 1997b, 1999). Possible factors that prevent most ants from evolving photoperiodic control of diapause are discussed by Kipyatkov (1996).

Thus, most temperate ant species rely upon internal clocks as well as on ambient temperatures in triggering the onset of diapause. In several endogenous-heterodynamic ants (most species belonging to genera *Aphaenogaster*, *Crematogaster*, *Lasius*, *Myrmica*, *Tapinoma*) environmental cues can alter the duration of the annual brood-rearing cycle within rather broad limits. For example, in *Myrmica rubra* and *M. ruginodis* short days and suboptimal temperatures of 17–20 °C in the middle of summer substantially advance the onset of diapause in larvae and queens (Kipyatkov 1974a, 1977a) while at long days and a temperature of 25 °C, which is well above the optimum of these species (21–22 °C according to Brian 1973), egg-laying by queens and the development and pupation of rapid brood larvae continues for several months without a break (Kipyatkov 1979, Kipyatkov & Lopatina 1997a). An example is given in Fig. 6.

The seasonal cycle of oviposition and development in other species is controlled predominantly by the endogenous mechanisms, and the time of the onset of diapause depends only slightly on environmental conditions in these ants. Thus, temperature hardly modifies the intrinsic length of the queens' oviposition period in all studied species of the genus *Formica* (Kipyatkov & Shenderova 1989, 1991, Kipyatkov & Lopatina 1993). The annual brood-rearing cycle in species belonging to the genus *Cataglyphis* and the subgenera *Camponotus s. str.* and *Leptothorax s. str.* is also comparably independent of the environment (Kipyatkov 1993, 1996, Kipyatkov & Lopatina 2002c).

FORMS AND PROPERTIES OF DIAPAUSE IN ENDOGENOUS-HETERODYNAMIC ANTS

Larval diapause

In most cases the diapause of larvae in ants is *facultative*, i.e. a given larva can either develop directly or enter diapause depending on the circumstances (Tab. 1). The diapause is induced by external factors and is normally ended due to diapause development at low temperatures (Kipyatkov 1993, 1996, Kipyatkov & Lopatina 2002c). In a few instances, however, the larval diapause can be obligate to some extent. Brian (1962, 1963) found that some *Myrmica* larvae emerging from the first eggs laid in spring had "a bias" for diapause and therefore they grew slowly, entered diapause and did not pupate without overwintering. Only at 24 °C and above could these larvae pupate if they were fed by workers with spring physiology (Brian 1963).

Evidently, temperature can affect larval development and induce diapause both directly and through the nurse workers, although the latter route has been investigated so far in only one instance. Brian (1955) carried out experiments with separate chilling of diapause larvae and workers of *M. ruginodis* and found that the process of vernalisation (see above) took place only in larvae, because larvae before overwintering never developed into alate females even if they were fed by workers in a spring state, whereas larvae subjected to cold and reared by autumn workers sometimes became alates under the relatively high temperature of 25 °C.

The ways by which the photoperiodic conditions can control larval diapause were studied in detail in *M. rubra* (Kipyatkov 1974b, 1976, 1981, 1988). Surprisingly, the larvae appeared to be entirely insensitive to the direct influence of photoperiods. Their development was instead controlled by workers who perceived the photoperiodic cues from the environment. Thus, non-diapause nurse workers (i.e. maintained under long days from the spring or activated by long-day photoperiods in autumn and, hence, physiologically active) stimulated rapid growth and pupation of summer larvae and terminated diapause in autumn larvae, whereas diapause workers (i.e. subjected to 3–4 weeks influence of short days and, hence, physiologically inactive) were unable to maintain a high growth rate of larvae and instead induced diapause in them (Kipyatkov 1974b).

In fact, this was an example of *social control of larval diapause by the workers*. However, the first case of such a control was described by Brian (1955) in *M. ruginodis*. He found that the spring workers (i.e. ants immediately following prolonged overwintering in a refrigerator) stimulated fast growth and pupation of diapause autumn larvae both at 20 and 25 °C. However, similar diapause larvae did not develop at all when fed by autumn workers (i.e. ants which performed a complete cycle of brood-rearing at optimal temperature during three months after overwintering). The results of Brian were then confirmed by Weir's (1959) experiments on the same species; Weir revealed also that young workers recently emerged from pupae were similar in their influence on larvae to the autumn workers. Plateaux (1971) made analogous experiments on *L. nylanderi* and showed that spring workers of that species are able to terminate diapause of autumn larvae. In subsequent experiments Brian (1963) found one more highly interesting form of social control of larval diapause: the stimulating effect of a queen whose presence in a culture led to a 4–5-fold increase of the percentage of pupating rapid brood larvae in comparison with ant cultures without queens.

Afterwards, Kipyatkov (1979) repeated experiments of Brian (1955) on *M. rubra* including naturally overwintered (spring) larvae as well. Spring larvae did not pupate at all under the care of diapause autumn workers, whereas naturally overwintered (spring) workers provoked growth and pupation in the majority of both spring and diapause autumn larvae. Significantly later we studied the phenomenon of worker social control in several ant species and made experiments according to the same exchange scheme with four combinations: (1) overwintered workers with overwintered larvae, (2) overwintered workers with diapause larvae, (3) diapause workers with overwintered larvae, (4) diapause workers with diapause larvae.

The results of these experiments differed significantly among species (Kipyatkov & Lopatina 1994, 1999, Kipyatkov et al. 1996, 1997). In *Camponotus herculeanus*, *C. japonicus* and several *Tetramorium* species non-overwintered diapause larvae fed by spring workers developed rapidly and pupated within a short period whereas overwintered larvae placed into the nests with autumn workers did not develop and pupate at all or only a few of them pupated sometimes. Thus, the workers of these ants exercise full control over the development and the diapause of their larvae. However, in *Leptothorax acervorum* we found an entirely opposite situation: autumn workers could not prevent development of spring larvae and they all pupated. At the same time overwintered workers stimulated development of less than half of diapause larvae. In *Myrmica rubra*, *M. ruginodis*, *M. lobicornis* and *Lasius niger* we observed an intermediate situation: only some spring larvae pupated when fed by autumn workers and also far from all autumn larvae finished development under the care of spring workers.

Thus, the forms of social influence on diapause by workers are diverse in ants and range from nearly absolute control (in *Camponotus* and *Tetramorium*), when the physiological state of workers completely defines the fate of larvae, to rather weak effects when diapause workers are unable to prevent the pupation of most overwintered larvae and spring workers are capable of inducing the development and pupation of only a few diapause autumn larvae (in *Leptothorax*). In most species (*Lasius*, *Myrmica*), however, the intermediate variants of diapause control are realized. There is some evidence that *Myrmica* workers can manipulate the development of larvae via changing the intensity of tactile stimulation and the frequency of feedings (Kipyatkov & Lopatina 1988, 1989a, b).

The stability of larval diapause differs significantly among ant species. In some species the diapause is quite stable and cannot be broken by the influence of high temperature and long days. Hölldobler (1961) observed that *C. herculeanus* and *C. ligniperda* larvae did not grow and stayed in diapause for a long time under high temperature. The same appeared true for *C. vagus* (Benois 1972). Passera (1969) showed that autumn larvae of *Plagiolepis pygmaea* did not grow even at high temperature and could pupate only after normal overwintering. We also found such stable larval diapause in several species of *Camponotus s. str.* as well as in *Camponotus aethiops*, *Plagiolepis compressus* and *Tapinoma erraticum*. The diapause larvae of all such species do not take food and grow while in diapause (Kipyatkov 1996, Kipyatkov & Lopatina 2002c).

At the same time, in many endogenous-heterodynamic species larval dormancy is unsteady and they all need lower temperature for diapause maintenance. Brian (1955) found that the diapause in autumn *Myrmica* larvae was rather unstable at 25 °C and many of them pupated in this situation. We observed such *thermal termination of diapause* with the pupation of almost all or of only part (depending on species) of diapause larvae in many endogenous-heterodynamic species belonging to the genera *Aphaenogaster*, *Crematogaster*, *Lasius*, *Lepisiota*, *Leptothorax*, *Manica* and *Myrmica*. Unlike the exogenous-heterodynamic species thermal termination of larval diapause in endogenous-heterodynamic ants occurs only at temperatures well above the optimum (Kipyatkov 1996, Kipyatkov & Lopatina 2002c).

In many ants, both endogenous- and exogenous-heterodynamic, which are characterised by diapause in the last larval instar, the diapause larvae continue to feed and to grow slowly and can attain a significantly larger size before overwintering. This trait was first recorded by Ezhikov (1929) in *Leptothorax* but it was Brian (1955, 1968) who first understood its significance. He found that such *diapause growth* plays a peculiar role in the process of caste differentiation in *Myrmica*. The diapause larvae grow in size but do not develop in fact, since their imaginal buds remain the same size and do not differentiate. Only such large diapause larvae well grown in autumn have the potential to develop into female reproductives in spring. Later, the same situation was discovered in *L. nylanderi* by Plateaux (1970). According to our data diapause growth is a property of species belonging to the genera *Diplorhoptrum, Lasius, Leptothorax, Lepisiota, Manica, Messor, Myrmica, Tetramorium, Camponotus* (some species), *Crematogaster* and *Monomorium* (Kipyatkov 1996, Kipyatkov & Lopatina 2002c).

Adult diapause

The winter dormancy is inevitable for all adult insects (except most winged reproductives) in a colony of temperate ants since all of them normally live for several years. Therefore, in the life cycle of each individual and of the colony as a whole the diapause arises and is completed repeatedly. Besides perennial social insects a recurrent reproductive diapause is known only in a few solitary species with diapause in the adult stage (Hodek 1979, 1983, 1998).

The adult diapause in endogenous-heterodynamic species is always *obligate* in a sense that it ensues sooner or later under any circumstances (Tab. 1). Environmental cues, such as temperature and photoperiod (in some species), can only advance or delay the onset of diapause to some extent. In many ant species diapause in queens and workers is not stable and can easily be interrupted by the influence of above-optimum temperatures. These species are exactly the same as those listed above that have unstable larval diapause. In ants having a photoperiodic influence on the induction of diapause, the diapause can easily be broken by exposure to long photoperiods. This so-called *photoperiodic termination of diapause* is well known in many insects, especially in species with diapause in the adult stage (Danilevskii 1961, Müller 1965, 1970, Hodek 1983, Danks 1987), and was found in our experiments in all *Myrmica* species studied (Kipyatkov 1972, 1977b, 1981, 1996, Kipyatkov & Lopatina 1997b, 1999) and in *Aphaenogaster sinensis* (Kipyatkov & Lopatina 1990).

At the same time, in some species the adult diapause is extremely stable and cannot be easily terminated by high temperatures and long days. Hölldobler (1961) first observed such stable diapause in queens of *C. herculeanus* and *C. ligniperda* kept at high temperatures. In experiments of Passera (1969) queens and workers of *Plagiolepis pygmaea* that had ceased to lay eggs at optimal temperatures did not start oviposition again without winter chilling. We found very stable queen diapause in the same species that had similarly stable larval diapause (listed above) and also in those species that pass winter without brood, i.e. in species of *Formica* and *Cataglyphis*, and also in *Ponera coarctata* (Kipyatkov 1996, Kipyatkov & Lopatina 2002c).

Adult ants, including workers and queens, while in the state of diapause, retain the ability to move freely and actively, to collect food, to feed themselves and other individuals, i.e. to behave as they usually do. The changes in behaviour connected with diapause in adult ants might exist, but this problem has not yet been studied except for one instance: diapause workers of *Myrmica rubra* are less aggressive and disposed to collect food in comparison with non-diapause ants (Kipyatkov 1976b).

During overwintering the diapause adults of most temperate ants are also able to move slowly at above zero temperatures. According to our observations, the cold coma temperatures in most northern ants during overwintering are usually about or slightly below zero. When ants in a cold coma are warmed up they immediately resume normal activity. All this was first observed by Holmquist (1928) in *Formica ulkei*. At the same time, some ants fall into a state of complete stupor, even deep lethargy, during overwintering, and they need a rather long period at warm conditions to awake completely from this cataleptic state. Holmquist (1928) first described this phenomenon in

Camponotus pennsylvanicus workers. We observed the same lethargic dormancy only in *C. herculeanus*, *C. ligniperda Harpagoxenus sublaevis* and *Leptothorax acervorum*.

Diapause of adults in insects is primarily reproductive diapause and is characterized by an inactive state of the reproductive system and by the inability of females to lay eggs (Danks 1987). This statement is also correct for ant queens and workers. Diapause queens do not lay eggs and their ovaries contain no eggs and developing oocytes during this period (Kipyatkov & Shenderova 1990, Kipyatkov 1996, Kipyatkov & Lopatina 2002c). Workers in most ants are also able to lay eggs, either fertile haploid eggs developing into males (when the queen is absent in a colony), or infertile trophic eggs (in the presence of a queen) to be used as food for larvae and queens (Hölldobler & Wilson 1990). Following overwintering the workers in cultures without queens normally lay fertile eggs during some period but then stop oviposition and stay in that diapause state for a long time. This was shown in *Myrmica ruginodis* (Brian 1953), *Plagiolepis pygmaea* (Passera 1969), *Leptothorax nylanderi* (Plateaux 1970), *Cataglyphis cursor* (Cagniant 1979, 1980) and in our experiments in *Lasius niger*, *L. flavus*, *L. acervorum*, *Tapinoma karavaievi* and several species of *Formica* (Kipyatkov 1996, Kipyatkov & Lopatina 2002c). Kneitz (1970) described the seasonal cycle in the state of worker ovaries in *Formica polyctena* and found that the percentage of workers with well-developed ovaries attained a maximum in July, but by October the ovaries in all workers became completely undeveloped, which is a good indication of diapause onset. After an exposure to short days the workers of *M. rubra* in cultures without queens did not lay eggs whereas they still produced eggs under long days (Kipyatkov 1976b).

Ambient temperature evidently affects all adult ants in a colony directly. We know nothing about possible indirect effects of temperature cues. However, photoperiodic cues act both directly and indirectly, i.e. by means of some mediators. Evidently, forager ants exiting from the nest for food are able to perceive photoperiodic cues directly, but they do not feed larvae themselves. How can the queens and nurse workers which normally never leave the nest perceive photoperiods? Could the photoperiodic response be realized if there were constant darkness inside the nest? In order to test this situation a special laboratory formicarium with a completely light-insulated nest chamber was constructed, where only workers were allowed to get out to the illuminated section but queens were prevented from doing so by a wire mesh at the exit hole. A quite normal photoperiodic response both during induction and termination of diapause was obtained in colonies of *M. rubra* kept in such formicaria (Kipyatkov 1976b). This means that if only some workers regularly leave completely dark nests it is sufficient for the effective photoperiodic control of diapause both in larvae and queens. We then tested whether workers could control diapause in queens the same way as they govern the development of larvae (see above). It was found that *M. rubra* queens were able to respond to photoperiodic cues themselves but the workers also very strongly affected their queens: non-diapause workers quickly terminated diapause in queens kept under short days but diapause workers only succeeded in decreasing the number of eggs laid by queens under long photoperiods (Kipyatkov 1976b). The physiological state of the queens is, thus, only under partial control of the workers in this species.

This form of social control of diapause was later investigated in some other ant species lacking photoperiodic responses. We used the same four combinations as in experiments with larvae (see above): (1) overwintered workers with overwintered queen(s), (2) overwintered workers with diapause queen(s), (3) diapause workers with overwintered queen(s), (4) diapause workers with diapause queen(s). In three *Formica* species the induction and termination of queen diapause proved to be completely free from worker influence, whereas in other ants (*Lasius niger*, *Tetramorium*) it was under partial control of workers, similar to *Myrmica*: spring workers were able to interrupt the diapause in queens but autumn workers could not prevent egg-laying by overwintered queens (Kipyatkov 1996).

An entirely new form of social control was also found in *L. acervorum*: spring larvae by unknown means affected queens and workers and terminated their diapause; as a result the workers activated by these larvae were able to provide adequate care and feeding not only for overwintered larvae but also for those larvae that originated from eggs laid by queens that had emerged from diapause; this response led to the unusual appearance of rapid-brood pupae in ant colonies without overwintering (Kipyatkov et al. 1997).

How do the forager workers in *M. rubra* colonies manage to transmit the information on photoperiodic cues from the outside of the nest to queens and nurse workers? Probably they use chemical mediators for this purpose. The existence of one such chemical signal was shown by Kipyatkov 1988, 2001). This substance was called *activator pheromone* since it terminated diapause in larvae and queens, i.e. exerted an activating effect on them. Unfortunately, no further experiments have been carried out in this very promising direction. In particular, we still do not know if there exists also an inhibitor pheromone causing the onset of diapause in larvae and queens.

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Variation in cold hardiness during overwintering in *Pyrrhocoris apterus* (Heteroptera: Pyrrhocoridae)

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Abstract. The seasonal variation in cold hardiness was studied in a field population of overwintering adults of the red firebug, *Pyrrhocoris apterus* (Linnaeus, 1758) from South Bohemia. Two processes/steps during the autumnal cold acclimation were distinguished: (1) in response to gradually decreasing temperatures *higher* than 5 °C, the supercooling point (SCP) decreased to a median of –18.6 °C, but the survival after exposure to –15 °C remained low ($Lt50_{-15}$ = 2.2 days); (2) during further cold acclimation at temperatures *lower* than 5 °C, the SCP remained relatively stable, but the capacity developed to survive at –15 °C for extended periods of time. Whereas the depression of SCP proved to be independent of the accumulation of 'winter' polyols (ribitol and sorbitol), there was a tight linear relationship (r = 0.95) between the total haemolymph concentration of winter polyols (seasonal max. = 88.9 mM) and the $Lt50_{-15}$ (seasonal max. = 17.5 days), which points toward a potential non-colligative cryoprotectant role for these compounds.

Heteroptera, Pyrrhocoris, diapause, cold hardiness, chill tolerance, supercooling, *cryoprotectants, polyols*

INTRODUCTION

In the Czech populations of the red firebug, *Pyrrhocoris apterus* (Linnaeus, 1758), the prevailing brachypterous individuals (Honěk 1976) enter reproductive diapause regulated by the neurohumoral system (Sláma 1964, Hodková 1976, 1979) in response to environmental cues such as short photoperiod, low temperature and high population density (Hodek 1968, 1983). The perception of sub-critically short days, during late summer and autumn, by the last-instar larvae and young adults was identified as the most probable way in which diapause is induced in the field (Hodek 1968). Diapause ends during December/January, and further development of the bugs is then prevented by low temperature (Hodek 1971, 1973). Overwintering adults of *P. apterus* can not tolerate freezing of their body fluids and rely on supercooling for winter survival (Hanzal 1988, Hodková & Hodek 1997). The temperature at which the body fluids start to crystallize (the supercooling point, SCP) sets the lower limit of survival and was found to be a reliable estimate of cold hardiness in *P. apterus* (Hodková & Hodek 1997). The capacity to survive low temperatures close to the SCP for extended periods of time (> 24 h), however, develops only gradually and thus, the maximum cold hardiness is attained with a certain delay after the SCP has reached its lower limit (Košťál & Šimek 2000). According to the classification proposed by Bale (1993), the overwintering *P. apterus* adults may be categorized as chill tolerant.

In this paper, the study of seasonal variation in cold hardiness in the field population of *P. apterus* is presented. Particular attention was paid to the autumnal cold acclimation and its effect on two apparently independent aspects or steps in the development of cold hardiness: the increase in supercooling capacity and the extension of survival time at sub-zero temperatures. Potential contributions of ribitol and sorbitol, which are accumulated during overwintering, to the seasonal changes in cold hardiness were assessed.

MATERIALS AND METHODS

Adults of *Pyrrhocoris apterus* (brachypterous form) were sampled during the cold season of 1999/2000 from a field population occurring near České Budějovice (49° N, 14° E; 400 m a. s. l.). All samples were taken in the morning and were kept at the outdoor temperature before processing. Only females were used in an attempt to obtain more homogenous results. Our previous study (Košťál & Šimek 2000) showed that females do not differ from males in the parameters assessed in this study.

Two parameters of cold hardiness, capacity for supercooling of body fluids and survival at –15 °C, were measured. The temperature of crystallization of body fluids (supercooling point, SCP) was measured as the lowest temperature achieved prior to the release of latent heat of crystallization during gradual cooling of the sample at a rate of 0.3 °C/min (Nedvěd et al. 1995). Survival after exposure to –15°C was assessed in samples of 10–20 females by placing them in a freezer (where temperature fluctuations did not exceed ± 0.5 °C) for various periods of time. After exposure to –15 °C, the bugs were transferred to 25 °C and a long day of 18L : 6D and their capacity for coordinated crawling was evaluated 7 days later. The temperature of –15 °C was selected purposely to make the survival test relatively 'hard'. Earlier results showed that (a) the temperature of –15 °C represents a minimum which may occur in the overwintering microhabitats of the Czech populations of *P. apterus*, (b) the overwintering adults of *P. apterus* can survive at such temperature, and (c) the criterion of coordinated crawling 7 days after exposure to –15 °C corresponds well to subsequent reproductive ability (Hodková & Hodek 1997, Košťál & Šimek 2000, Košťál, unpublished results). The time of exposure, after which 50% of the individuals survived ($Lt50_{-15}$), was estimated using nonlinear regression. Either the logistic sigmoid or exponential decay curves were constructed to obtain the best fit to the survival data. The equations were:

sigmoid: $S(t) = L \times \{\exp[A \times (1 - t/Lt50_{-15})]\}/\{1 + \exp[A \times (1 - t/Lt50_{-15})]\}$

exponential: $S(t) = L \times \exp(-t/Lt50_{-15})$

where S is the survival (0 to 1.0), parameter L introduces the initial level of survival (y axis intercept), parameter A influences the slope of the middle part of the sigmoid curve, and t is the time of exposure. In theory, the exponential decay of survival curve signals that the main cause of death will be stochastic occurrence of freezing in the metastable supercooled body fluids (Salt 1961) and the sigmoid pattern indicates that cumulative cold injury is the main cause of death (Nedvěd et al. 1998).

The haemolymph samples were collected from five females by cutting off one of their antennae and bleeding into a capillary tube. The concentrations of two major polyols that accumulate during overwintering, ribitol and sorbitol (Košťál & Šimek 2000), were measured by gas chromatography coupled to mass spectrometry as described earlier (Košťál & Šimek 1995).

The daily minimum and maximum air temperature data (Fig. 1a) were obtained from a meteorology station (Czech Institute of Hydrometeorology) located ca. 1 km from the field site.

RESULTS

Supercooling

The SCP (Fig. 1b) was extremely variable in late summer (20 September), ranging from –4 to –20 °C with a median value of –12.9 °C. In early November, the median SCP moved to –18.6 °C. On November 23, the SCP was not measured, but as *P. apterus* can not survive at temperatures below the SCP (Hodková & Hodek 1997), more than 77% of the individuals must have had an SCP lower than –15 °C because they were able to survive at such a temperature for 24 h (see Fig. 2). One week later, on November 30, the median SCP was –20.5 °C. In mid-January, the median SCP value must have been lower than –15 °C in some 87% of females according to the estimate based on survival data (Fig. 2). The samples collected in February and March showed a trend of increasing median SCP, nevertheless, a certain proportion of individuals had an SCP below –15 °C.

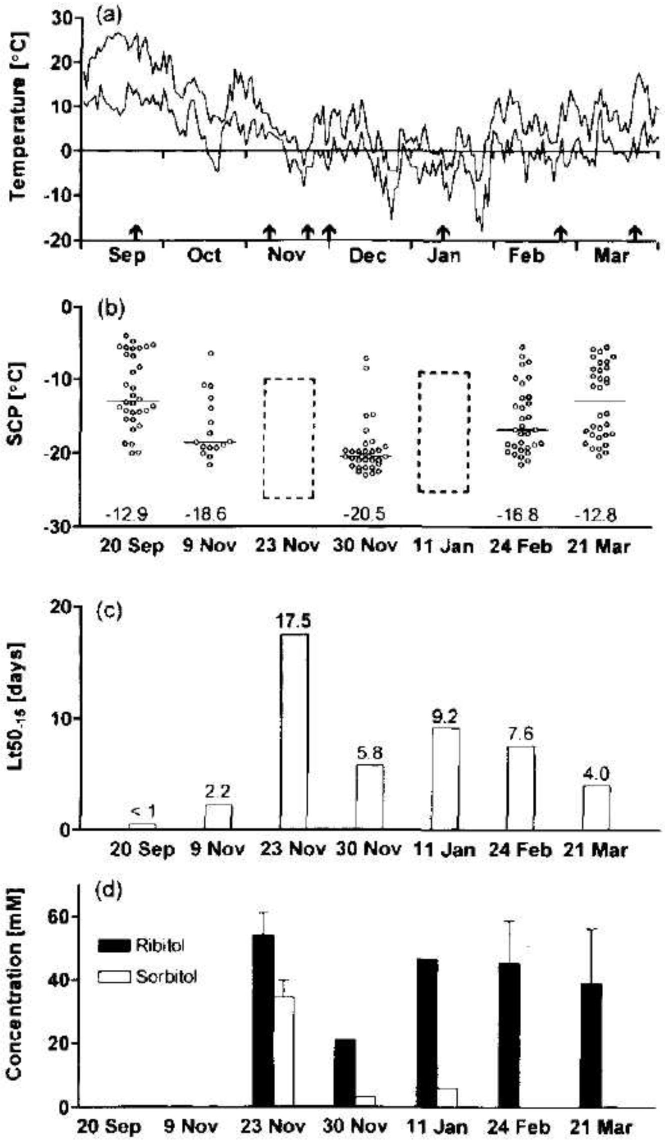

Fig. 1. Summary of results. (a) trend in the daily maximum and minimum temperatures from September 1999 to March 2000 at České Budějovice, South Bohemia. The arrows indicate the dates on which adults of *Pyrrhocoris apterus* (L.) were collected in the field. (b) Seasonal changes in supercooling point (SCP); individual data points and median value (horizontal line, numeric value) are depicted. No measurements were made on 23 November and 11 January (rectangles). (c) Seasonal changes in cold hardiness measured as the period of exposure to −15°C, after which 50% of the individuals survived ($Lt50_{-15}$); $Lt50_{-15}$ was calculated using nonlinear regression (see Materials and Methods), the regression curves are characterized in Tab. 1 and depicted in Fig. 2. (d) Seasonal changes in haemolymph concentrations of ribitol and sorbitol measured by gas chromatography coupled to mass spectrometry; each column represents either a mean of $n = 5$ individuals measured independently (the vertical bars represent *S.E.*) or a result of one measurement of a sample pooled from 5 individuals (no *S.E.* bars).

Tab. 1. Parameters of the survival curves depicted in Fig. 2. Where missing, the value could not be calculated. The values of $Lt50_{-15}$ followed by different letters were significantly different (ANOVA: $F = 5.93$, $P = 0.0006$; followed by Tukey's Multiple Comparison Test)

Sampling date	Shape	Parameters L	A	$Lt50_{-15}$ ± $S.E.$⁽¹⁾	Proportion of variance accounted for [%]
20 Sep	–	–	–	–	–
9 Nov	sigmoid	0.80	6.56	2.19 ± 0.12 c	99
23 Nov	sigmoid	0.83	2.55	17.51 ± 4.05 ab	62
30 Nov	exponential	0.88	–	5.77 ± 2.15 c	77
11 Jan	exponential	0.92	–	9.20 ± 2.84 bc	70
24 Feb	sigmoid	0.51	18.23	7.64 ± 0.53 c	58
21 Mar	sigmoid	0.40	4.06	3.99 ± 0.47 c	99

Survival

On September 20, none of the females survived after exposure to −15 °C for 24 h (Fig. 1c) despite the fact that the SCP was lower than −15 °C in some of them (see Fig. 1b). On November 9, although the SCP was lower than −15 °C in most females, the $Lt50_{-15}$ was relatively short (2.2 days). The $Lt50_{-15}$ was considerably longer (17.5 days) two weeks later, on November 23, but decreased again to 5.8 days one week later, on November 30. The $Lt50_{-15}$ of 9.2 days was recorded in the sample taken during January and a gradual decrease of $Lt50_{-15}$ was observed during February and March (Fig. 1c).

Surival curves are depicted in Fig. 2 and relevant parameters are summarized in Tab. 1. The parameter L indicates the proportion of females having an SCP lower than −15 °C; such females either survived or died during exposure to −15 °C (see $Lt50_{-15}$), either due to occurence of stochastic freezing or due to cumulation of a 'chill injury' (i.e. without freezing).

Polyols

Traces of ribitol and sorbitol (< 50 nM) were detected in the haemolymph of females collected on September 20 and on November 9. Only fourteen days later, on November 23, 54.3 mM of ribitol

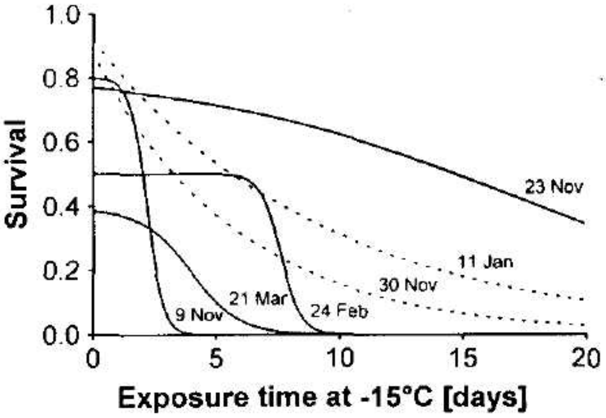

Fig. 2. The decrease in survival with increasing time of exposure to −15 °C in the overwintering adults of *Pyrrhocoris apterus* (L.). The sampling dates are shown. The survival curves were obtained using nonlinear regression (see Materials and Methods) and are further characterized in Tab. 1.

and 34.6 mM of sorbitol were found in the haemolymph. Within the subsequent week the concentrations dropped to 21.2 and 3.2 mM of ribitol and sorbitol, respectively. January females showed slightly elevated concentrations of both polyols (ribitol, 46.7 mM; sorbitol 6.1 mM). While ribitol was still present at relatively high amounts in the February and March samples, only traces of sorbitol were detected (Fig. 1d).

DISCUSSION

In this paper, the natural seasonal variation in cold hardiness of overwintering adults of *Pyrrhocoris apterus* was described. Females collected during the late summer, on September 20, were in reproductive diapause (Hodek 1968) but had not experienced any substantial fall of temperature because the night minima seldom fell below 10 °C and the day maxima regularly reached about 25 °C. The values of SCP were widely scattered around a median of –12.9 °C, which is typical for diapausing bugs prior to cold acclimation (Hodková & Hodek 1997). Although the SCP was lower than –15 °C in some individuals, they showed a very limited capacity (< 24 h) to survive at this temperature. Only traces of 'winter' polyols, ribitol and sorbitol (Košťál & Šimek 2000), were found in the haemolypmh. During October, the air tempeatures gradually decreased, nevertheless, they only seldom dropped below 5 °C, which is the upper temperature threshold for rapid accumulation of polyols in many insects (see Storey & Storey 1991 for review) including *P. apterus* (Košťál, unpublished data). In response to decreasing environmental temperature, the SCP dropped to –18.6 °C already by November 9. The $Lt50_{-15}$, however, remained relatively short (2.2 days) and still almost no 'winter' polyols were present in haemolymph. Between November 9 and 23, the night minima dropped below zero and day maxima did not exceed 5 °C. Such temperatures favour the accumulation of cryoprotectants and indeed, 54.3 mM of ribitol and 34.6 mM of sorbitol were detected in the sample of 23 November. Interestingly, within the same fourteen days, the $Lt50_{-15}$ considerably increased to 17.5 days without any substantial depression of the SCP. Such a tight temporal coincidence between accumulation of polyols and development of cold hardiness (namely extension of $Lt50_{-15}$) may suggest that a causal relationship exists between the two. This suggestion is further supported by subsequent co-development of both features. Within a week from 23 to 30 November a warmer spell occurred. Although the night minima remained below zero, the day

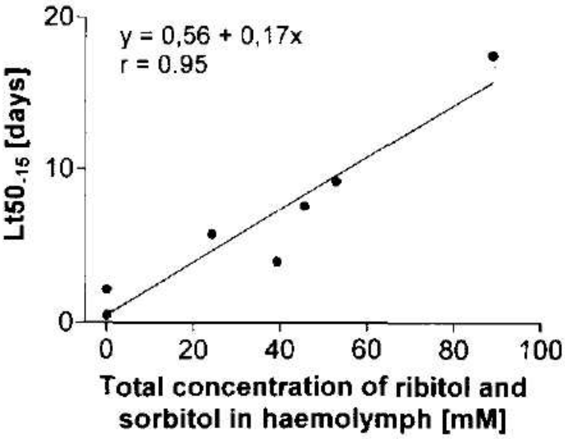

Fig. 3. The linear relationship between the total concentration of polyols in haemolymph and the $Lt50_{-15}$ of overwintering adults of *Pyrrhocoris apterus* (L.).

maxima reached 10 °C and the bugs were active throughout the days, basking on the bases of tree trunks in large clusters, and rapidly moving when disturbed. The sample of 30 November showed no substantial change in SCP, which documents the relative stability of this feature. However, the concentration of polyols, and the *Lt50* $_{-15}$ decreased considerably. The samples collected during January, February and March revealed a gradual loss of supercooling capacity, decrease of *Lt50* $_{-15}$, and depletion of polyols. The relationship between the total concentration of both polyols in the haemolymph and the *Lt50* $_{-15}$ was described by a linear regression with high correlation coefficient $r = 0.95$ (Fig. 3).

The results presented here suggest that two independent processes or steps in the autumnal development of cold hardiness can be distinguished in *P. apterus* and, perhaps, in some other chill tolerant overwintering insects as well: (1st step) in response to gradual cold acclimation at temperatures *higher* than 5 °C, the SCP is depressed and the capacity for short-time (<24 h) survival at temperatures slightly above the SCP develops concomitantly; (2nd step) during further cold acclimation at temperatures *lower* than 5 °C, the SCP does not change but the capacity develops to survive for extended periods of time at temperatures slightly above the SCP.

Whereas the depression of SCP was obviously independent of the accumulation of polyols, the seasonal fluctuations in *Lt50* $_{-15}$ were tightly correlated with fluctuations in the haemolymph concentrations of polyols. The accumulation of various polyols is observed in many chill tolerant overwintering insects (see Sømme 1982, Lee 1991 for examples). When polyols are present at high concentrations (ca. >1M), colligative properties (e.g. melting and supercooling points) are affected significantly (Zachariassen, 1985). This is not the case for *P. apterus* where the concentrations of polyols in the haemolymph were too low to bring about any substantial depression of melting and supercooling points. It is known that certain solutes, including low molecular weight sugars and polyols, may protect/stabilize the conformation of proteins in aqueous solutions and thus ensure their proper functioning at low temperatures (Carpenter & Crowe 1988). Further work will be necessary to elucidate whether the tight correlation between *Lt50* $_{-15}$ and concentration of polyols in *P. apterus* signals a causal relationship or a mere temporal coincidence between two independent phenomena.

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BOOK REVIEW

BECKER W. M., KLEINSMITH L. J., HARDIN J.: **The World of the Cell.** Fourth edition. The Benjamin/Cummings Publishing Company, an imprint of Addison Wesley Longman: San Francisco, Reading, New York, Harlow, Don Mills, Sydney, Mexico City, Madrid, Amsterdam, 2000. XXXII+878 pages. Format 215×273 mm. Hard cover. Price USD 94.00. ISBN 0-8053-4531-0

The authors are acknowledged professionals affiliated with Universities of Wisconsin and Michigan. As stated in the preface, past several decades have witnessed an explosive growth in our understanding of the properties and functions of living cells. First edition of this book appeared in 1986. The authors have tried to retain the features of the first three editions that readers have identified as "user-friendly" while still reorganizing and updating the material. In the introductory text there is an alphabethical *Guide to Techniques and Methods*. The volume consists of five parts composed of 23 chapters subdivided into conceptual sections. Each chapter contains a list of *Key Terms* for self-testing and a list of *Suggested Reading*: articles that are especially relevant to the topics of the chapter. More challenging problems are included in a *Problem Set*. In addition, *Boxed Essays* provide insights into difficult principles and contemporary techniques of cell biologists. Textual parts are illuminated by abundant two- and three-dimensional figures presented mostly in full colour.

Part One (chapters 1 through 6) introduces **The World of the Cell: an Overview of Structure and Function** as delineating the chemistry and macromolecules of the cell, organelles, the flow of energy in the cell, and enzymes: the catalysts of life. **Part Two** (chapters 7 through 12) gives attention to **Membranes and Cell Signaling.** In this part analyzed are the structure, function and chemistry of membranes, transport across membranes, particularly the overcoming of permeability barrier, signal transduction mechanisms, namely electrical signal in nerve cells, messengers and receptors. Subsequent chapters discuss structural and functional aspects of cell-to-cell contacts: extracellular structures, cell adhezion, and cell junctions, furthermore the intracellular compartments: endoplasmic reticulum, Golgi complex, endosomes, lysosomes, and peroxisomes. **Part Three** (chapters 13 through 15) focuses on **Energy Flow in the Cell**, especially on the sources of energy available to the biological world and the processes of energy conversion and utilization in cells, on aerobic respiration and on phototrophic energy metabolism. **Part Four** (chapters 16 through 21) outlines the **Information Flow in Cell.** These six chapters are devoted to the structural basis of cellular information presented by DNA, chromosomes, the nucleus, and to an overview of the cell cycle, DNA replication, damage and repair, nuclear and cell division, gene control and cancer. In following chapter looked at are sexual reproduction including meiosis and generic recombination. Finally, treated are miscellaneous aspects of gene expression: the genetic code and transcription, protein synthesis and sorting, gene regulation and genomic control. **Part Five** (chapters 22 and 23) concentrates on **The Cytoskeleton and Cell Motility**. Described are major structural elements of the cytoskeleton of eukaryotic cells: microtubules, microfilaments and intermediate filaments. Cellular movement ensures coverage of motile systems, intracellular microtubule-based movement: kinesin and dynein, microtubule based motility, actin- and filament-based movement in muscle and nonmuscle cells. In an appendix principles and techniques of microscopy are explored. This closing essay deals with optical principles of microscopy, the light microscope and a variety of microscopical techniques: brightfield microscopy, phase-contrast microscopy, differential interference contrast, fluorescence microscopy, confocal scanning microscope and digital video microscope. In addition, the electron microscope and sample preparation techniques are incorporated.

Written in a readable and attractive style, this most comprehensive handbook offers invaluable tools to aid the reader in understanding of particularly important and intriguing aspects of modern cell biology.

Jindřich Jíra

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Survival under dry conditions of males, and diapause and non-diapause females of the predatory mite *Euseius finlandicus* (Acari: Phytoseiidae)

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Abstract Survival under dry conditions of males and of diapause and non-diapause females of the predatory mite ***Euseius finlandicus*** (Oudemans, 1915) that developed under a short or a long day photoperiod, respectively, was studied. Females in diapause survived significantly longer than that not in diapause. Males survived for a significantly shorter period than both diapause and non-diapause females. The high tolerance of dry conditions in diapause females is apparently related to the risk of dehydration during hibernation.

Diapause, resistance to drought, desiccation, Phytoseiidae, *Euseius finlandicus*

INTRODUCTION

The predatory mite *Euseius* (syn.: *Amblyseius*) *finlandicus* (Oudemans, 1915) (Acari: Phytoseiidae) is widely distributed and has been recorded in many countries throughout Europe, Asia and North America (Kropczynska & Petanovic 1987, Kropczynska & Tuovinen 1988, McMurtry & Croft 1997). The mite has a typical mesostigmatic life cycle with an egg, three active immature stages (larva, protonymph and deutonymph) and an adult (Sabelis 1985). As in all phytoseiid mites in temperate regions, adult females overwinter in reproductive diapause (Overmeer 1985, Veerman 1992 and references therein).

In several insect species, diapause is associated with an increase in desiccation tolerance (Danks 2000). Increased desiccation tolerance may be due either to a reduction of water loss, mainly by the production of copious amounts of cuticular wax, or to the ability of the resistant individuals to withstand substantial water loss and survive even if they are extensively dehydrated. In general, non diapause phytoseiid mites depend on a high ambient relative humidity (RH) for succesful development and reproduction (e.g., Dinh et al. 1988, Bakker et al. 1993), although *Typhlodromus occidentalis* (Nesbitt, 1951) shows a remarkable tolerance to low relative humidity (Yoder 1998). Phytoseiid females in diapause do not feed or drink water (Veerman 1992), therefore, their survival during hibernation may depend on desiccation tolerance in addition to cold hardiness, which is well documented (e.g., Van der Geest et al. 1991 for *Amblyseius andersoni* (Chant, 1957), Broufas & Koveos 2000 for *E. finlandicus*).

In this paper, survival in dry conditions of diapause and non-diapause females, and males of *E. finlandicus*, reared under laboratory conditions, were evaluated and compared.

MATERIALS AND METHODS

The mite

The colony of *E. finlandicus* used in these experiments was established with mites collected from a cherry orchard in the area of Naousa, northern Greece, in 1996. The colony is maintained in the laboratory at 24°C and

Tab. 1. Time (hours) to 50% mortality (Lt_{50}) at a low RH (<10%) and 20 °C of diapause and non-diapause females and males of *E. finlandicus* (Oudemans) reared under short day (LD 8:16) or long day (LD 16:8) condotions.

	n	Slope±SE	Lt_{50}	95%CL	χ^{2*}
Individuals developed under LD 8:16 and 20 °C					
Diapause females	**780**	12.19±0.82	66.4 a	65.2–67.7	12.73
Males	**480**	13.85±1.07	13.2 b	12.9–13.4	3.75
Individuals developed under LD 16:8 and 20 °C					
Non-diapause females	780	14.80±0.87	23.0 c	22.6–23.4	14.46
Males	480	14.15±1.08	13.1 b	12.6–13.6	12.65

* no χ-square values significant (P= 0.05)

a photoperiod of LD 16:8 on detached bean leaves. *Typha* sp. pollen was provided as food for the mites, as described by Broufas & Koveos (2000).

For the experiments, groups of approximately 30 adult females from the main stock colony were transferred to fresh bean leaves and allowed to lay eggs for 24 h at 24 °C. Subsequently, the leaves with the eggs were maintained at 20°C and a photoperiod of either LD 8:16 or LD 16:8, until the mites completed their entire embryonic and post-embryonic development. *Typha* sp. pollen enriched with 5% b-carotene was added twice per week to the leaf surface as food for the immature and adult mites. Under the short-day photoperiod, all the females entered diapause, whereas under the long-day photoperiod, they laid eggs and did not enter diapause. When 10 days old, adult females and males were used in the experiments.

Survival under dry conditions

Experimental mites were placed in groups of 20 individuals in small cages. The cages consisted of small cylindrical gelatin capsules (9×5 mm). One side of the capsule was removed and in its place a fine polyester mesh was attached which allowed proper ventilation inside the capsule but prevented the escape of the mites. Desiccation stress was applied by placing the cages with the mites in small petri dishes (~ 5 cm in diameter) with fresh dried silica gel at their bottom. The lid of each dish was closed with a strip of parafilm to prevent the absorption of water vapors from the surrounding air. Inside each Petri dish the RH fell below 10% in 1h and then gradually decreased further.

Subsequently, the Petri dishes with the mites were placed at 20 °C and at the same diapause-inducing or diapause-averting photoperiod used during the preimaginal stages and early adult life of each group. At different time intervals, 6 groups of 20 males and females developed under diapause-inducing and diapause-averting conditions were removed from the petri dishes and mortality was assessed. As dead were considered those mites that could not walk after probing them with a fine camel hair brush. Six groups of 20 females or males were used as control, exposed to water vapor saturated atmosphere inside closed petri dishes with a wet cotton wool at their bottom.

Probit analysis was used to estimate the lethal time (Lt_{50}) for 50% mortality of females and males developed under the different photoperiodic conditions. The Lt_{50} values were used as indices for resistance at dry conditions. Differences in Lt_{50} of different experimental groups were considered statistically significant if the 95% fiducial limits did not overlap (Finney 1952).

RESULTS AND DISCUSSION

Diapause females of *E. finlandicus*, which developed under a short-day photoperiod of LD 8:16 survived significantly longer under dry conditions than non-diapause females, which developed under a long-day photoperiod of LD 16:8 (Fig. 1, Tab. 1). In diapause females mortality was very low even after 54h of exposure to dry conditions. After longer exposures, it increased gradually and reached 100% after 98h. In contrast, in non-diapause females mortality increased from 5 to 100% after 18h and 33h of exposure to the same dry conditions (Fig. 1). The time to 50% mortality (Lt_{50}) was 23h for non-diapause females and approximately three times longer (66.4h) for diapause females (Tab. 1). The significantly greater survival in time at dry conditions of diapausig in relation to non-diapausing females may be linked to various features of diapause such as increased epicuticular lipids, or reduced respiration and metabolism, as recorded for a number of insect species (Danks 1987, 2000). In winter, diapause females of *E. finlandicus* are found mainly in cracks, crevices and other protected places on the trunks, branches and twigs of plants, usually in small groups, which do not move or feed (Broufas & Koveos, unpublished). Therefore, diapause females do not take up water by feeding or contact with leaf surfaces and their ability to survive at dry conditions for long

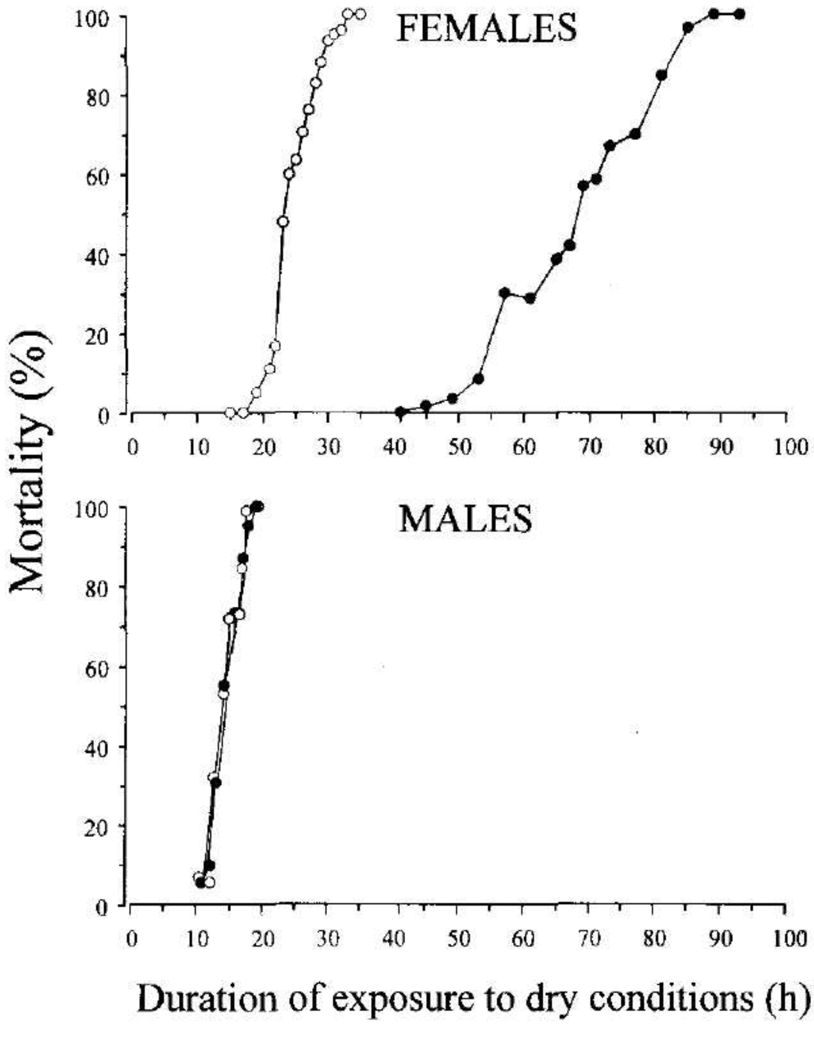

Fig. 1. Mortality percentages after various periods of time under low RH (<10%) conditions at 20 °C of diapause and non-diapause females and males of *E. finlandicus* developed from egg to adult at two photoperiods and 20°C (open circles: non-diapause females or males developed under a photoperiod of LD 16:8; closed circles: diapause females or males developed under LD 8:16).

periods which apparently reflects a high desiccation tolerance plays a major role for survival during winter. It is known that non-diapause phytoseiid mites can use water vapour from the air (Yoder 1998 and references therein). Therefore, we may assume that, besides their high dry tolerance, diapause females can absorb water from the air during winter, especially when RH is high. In addition, cold tolerance is also important role for survival of this mite during winter (Broufas & Koveos 2000). Differences in survival under dry conditions and desiccation tolerance between diapause and non-diapause individuals have been found in a few insect species (e.g., Sota & Mogi 1992 for mosquito eggs; Gehrken & Doumbia 1996 for grashopper eggs). Desiccation tolerance has been studied for non-diapause females of the phytoseiid mites *T. occidentalis* and *E. finlandicus*. Due to their lower water loss rate, females of *T. occidentalis* were found to be more resistant than those of *E. finlandicus* (Yoder 1998).

Males of *E. finlandicus* developed under either a long or a short-day photoperiod survived for a significantly shorter period under dry conditions than similarly developed and treated females (Fig. 1, Tab. 1). Both short and long-day-developed males showed a similar trend in mortality with time of exposure to dry conditions. The Lt_{50} for short and long-day developed males was 13.2h and 13.1h respectively and significantly shorter than the respective values of females (Tab. 1). Mortality in the control groups, i.e. females or males exposed to water vapor saturated atmosphere, was less than 5% (not shown in the figure).

The significantly higher survival time at dry conditions of females in comparison to males may be due to differences in size between the sexes. Phytoseiid females are larger than males (Schulten 1985), therefore, the surface to volume ratio may be smaller in females. Thus, water loss in relation to body mass is expected to be lower in females than in males. Similar differences in survival under dry conditions between females and males have been found in a number of insect species such as *Drosophila triauraria* (Goto et al. 1997) and *Zaprionus* sp. (Barker & Barker 1980). Similarly, larger eggs of *Aëdes* mosquitoes are more tolerant to desiccation than smaller ones of the same species (Sota & Mogi 1992).

In conclusion, diapause females of *E. finlandicus* are highly tolerant of dry conditions, an adaptation which may play an important role in their survival during winter. In addition, previous work has shown that a significant increase in cold tolerance occurs in females after diapause induction (Broufas & Koveos 2000). We may assume that dry and cold tolerance may be based on the same or similar biochemical or physiological processes activated after diapause induction. Further experiments are needed to cast light on this matter.

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BOOK REVIEW

HARTWELL L. H., HOOD L., GOLDBERG M. L., REYNOLDS A. E., SILVER L. M., VERES R. C.: **Genetics: from Genes to Genomes.** McGraw-Hill Higher Education, a Division of the McGraw-Hill Companies: Boston, Burr Ridge, Dubuque, Madison, New York, San Francisco, St. Louis, Bangkok, Bogotá, Caracas, Lisbon, London, Madrid, etc., 2000. XXIII+820 pages, brief answer section 10 pages, glossary 13 pages, credits 4 pages, index 18 pages. Format 215×275 mm. Hard cover. Price USD 80.00. ISBN 0-07-540923-2

First author is president and director of the Fred Hutchinson Cancer Research Center, the other authors are acknowledged experts affiliated with US universities. The prologue outlines the central themes of genetics and establishes the foundation of integrated presentation of Mendelian and molecular genetics. The volume consists of VII parts divided into 24 chapters.

Part I (chapters 1 through 4) on the **Basic Principles: How Traits Are Transmitted** provides presentation of Mendelian genetics, patterns, particles, and principles of heredity, extensions to Mendel complexity in relating genotype to phenotype, the chromosome theory of inheritance, and linkage, recombination and the mapping of genes on chromosomes. **Part II** (chapters 5 through 7) accentuates **What Genes Are and What They Do** while analyzing how the molecule of heredity carries, replicates and recombines information. Furthermore, delineated are the anatomy and function of gene: dissection through mutation, and gene expression: the flow of genetic information from DNA via RNA to protein. **Part III** (chapters 8 through 10) gives attention to the **Using of Genetic Engeneering to Unravel the Information in Genomes** and includes the use of recombinant DNA technology and hybridization as tools of genetic analysis, the direct detection of genotype, and the mapping and analysis of genomes.

Part IV (chapters 11 through 14) on **How Genes Travel** examines the molecular mechanisms underlying the chromosomal transmission of genetic information in eukaryotes and prokaryotes: the eukaryotic chromosome as an organelle for packaging and managing DNA, chromosomal rearrangements and changes in chromosome number, genetic analysis in bacteria, and the non-Mendelian patterns of inheritance. **Part V** (chapters 15 through 17) explores **How genes Are Regulated** as describing gene regulations in prokaryotes and eukaryotes as well as the cell cycle regulation and the genetics of cancer. **Part VI** (chapters 18 through 22) focuses on **Gene Regulation and Development: Portraits of Model Eukaryotic Organisms**. In these chapters attention is given to five model organisms that have become prototypes for research in developmental genetics. Among other topics discussed are the relatedness of all organisms and the genetic methods that enable to answer the questions of developmental genetics. **Part VII** (chapters 23 and 24) concentrates on **How Genes Change**, namely on the genetic analysis of populations and how they change, and on evolution at the molecular level.

The epiloque discusses **Human Genetics and the Future of Biology**. This closing essay emphasizes that human genetics is emerging as the overarching field of biomedical research. Biology is now a science based on molecular information and on genomic and protein analysis. In the back of the text, the authors provide two appendices: guidelines for gene nomenclature and a section containing answers to selected end-of-chapter problems. Furthermore, a comprehensive glossary includes terms relevant to genetics.

This volume is amply illustrated by a wealth of figures presenting – mostly in colour – two- and three-dimensional and space-filling models and arrangements of molecules and structures. Numerous tables offer overviews of presented data. This most remarkable book integrates formal genetics, molecular genetics, genomics and information science, human genetics, synthesis from many different organisms, and molecular evolution into one coherent whole.

Jindřich Jira

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Temperature Relations of Egg Diapause in Two Species of Camel Cricket with Biennial Life Cycles (Orthoptera: Rhaphidophoridae)

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Abstract. Eggs of two species of camel cricket *Atachycines apicalis* (Brunner, 1888) (= *Aa*) and *Tachycines asynamorus* Adelung, 1902 (= *Ta*) enter diapause soon after deposition. When exposed to various constant temperatures, they hatched at 15–25 °C and the hatchability at 20 and 25 °C was higher in *Aa* than in *Ta* but the reverse was the case at 15 °C. Exposure to temperatures of 4–20 °C for vaious periods followed by incubation at 25 °C resulted in three groups of eggs: (a) hatched in =7 weeks, (b) hatched in >7 and <30 weeks and (c) unhatched for >=30 weeks. The proportion of 'a' eggs was increased by previous exposure to 10–20 °C in *Aa* and to 7–15 °C in *Ta*. Nymphs of various sizes (and sometimes adults) were caught occasionally (*Aa*) or by traps (*Ta*) shortly before and after winter. From these data, both species are inferred to have biennial life cycles, passing the first winter as eggs and the second winter as larvae or even adults. The different thermal requirements in the egg stage of the two species cannot as yet be related to their different habitat preferences.

Egg diapause, thermal response, camel crickets, Orthoptera, Rhaphidophoridae,*Tachycines asynamorus*, *Atachycines apicalis*

INTRODUCTION

The camel crickets are among the least studied groups of Orthoptera and little is known about their dormancy, although their relatives, cave crickets, have been well studied (Di Russo et al. 1994). Descriptions of the seasonal life cycles of camel crickets are contradictory. Ito et al. (1977) wrote that the two common species *Tachycines asynamorus* Adelung 1902 and *Atachycines apicalis* (Brunner 1888) overwinter in the egg and nymphal stages, while Kobayashi (1981) described that the latter as univoltine and overwintering as middle-stage nymphs.

In Hirosaki, nymphs of *A. apicalis* are found on the forest floor, in sewers and wells, around houses and under floors. In autumn, they may enter houses, probably in search of shelter for overwintering. They are variable in size, apparently belonging to different instars (unpublished observations).

T. asynamorus was found in a university greenhouse. This species is ecologically somewhat different from *A. apicalis*. It occurs more frequently in houses than the latter, particularly greenhouses and is widely distributed in Eurasia and has been introduced into North America. In Japan, it is thought to be an immigrant from China (Ichikawa 1997).

We tried to elucidate the factors involved in the regulation of life-cycle of these species and started to analyze the thermal relations of their egg stages.

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Tab. 1. Fate of eggs of *Atachycines apicalis* (Brunner) kept at constant temperatures for 200 days from deposition

Temper. (°C)	Number of eggs	With eyespots (%)	Hatched (%)	Hatchingtime*	Died (%)
4	120	0.0	0.0	–	16.7
7	110	0.0	0.0	–	12.7
10	119	21.8	0.0	–	16.8
15	110	58.2	18.2	181±17.2	17.3
20	108	85.2	82.4	144±15.9	12.0
25	153	75.8	75.2	121±15.7	11.7
30	137	0.0	0.0	–	11.1
35	97	0.0	0.0	–	100.0

*Mean ± SD days. The real mean and SD at 15°C were much larger than shown as suggested by Fig. 1A.

MATERIALS AND METHODS

Rearing adults and collecting eggs

Large nymphs of *Atachycines apicalis* were collected in April and May 1992 from sewers, and those of *T. asynamorus* in February 1992 and later from a greenhouse, both in the university grounds. They were reared in plastic aquaria (W23×L43×H28 cm) kept at about 25 °C and under natural daylength conditions. The bottom of each aquarium was lined with sheets of paper, and several loosely corrugated sheets of paper were provided as shelters. Commercial insect food (Oriental Yeast Industry Co.), dry wheat germ (Nisshin Seifun Co.), slices of carrot, and cut cabbage moth pupae were given as food. Cotton-plugged water bottles provided a source of water supply.

For oviposition, dishes of moist fine sand were placed in each aquarium, but adults deposited more eggs in the cotton plug of the water bottle than in the sand. Eggs were collected every two days and laid on moist layers of cotton wool in plastic containers. The hatchlings and dead eggs (discoloured or collapsed) were counted and removed daily.

Temperature treatments

To determine the range of temperatures at which eggs will develop, newly laid eggs were kept in the dark at one of eight constant temperatures ranging from 4 to 35 °C, and the number of hatchlings were recorded every day for more than 200 days. These experiments revelaed that eggs of both species underwent diapause.

The next series of experiments was designed to assess the effect of low temperature on diapause termination. Eggs were exposed to 4, 7, 10, 15 and 20 °C for 2 to 15 weeks, then incubated at 25 °C. Hatchlings and dead eggs were counted, and removed every day.

A third series of experiments using *T. asynamorus* eggs was designed to determine their response to temperature in the late diapause or the postdiapause stages. Newly laid eggs were first exposed to 10 °C for 8 weeks and then transferred to 15, 20, 25 and 30 °C. Other procedures were the same as described above.

Stage composition of *T. asynamorus* in a greenhouse

We placed two baited traps in a greenhouse, where the temperature was kept at about 20 °C in the day and at about 15 °C at night from November to April, but no air conditioning was available in the summer. The trap was made of a 1.5 litre plastic bottle; the top funnel-shaped part was cut, inverted and inserted, and fixed, into the cylindrical portion. Each trap was baited with a wheat germ diet and the inner side was smered with margerine. The traps were examined every week and trapped insects were counted and released on the spot.

RESULTS

Development at constant temperatures

In both species, eggs survived the exposure to 4 and 7 °C for more than 200 days, but were only able to hatch at temperatures of 15 °C and higher. At 10 °C, none had hatched after more than 200 days, though eggs did develop to the stage at which the pigmented eyes could be seen as dark spots through the chorion (Tabs 1, 2). On the other hand, a few eggs of *T. asynamorus* hatched at 30 °C but none of *A. apicalis*, although the mortality was not high in both species at 30 °C. All eggs died at 35 °C.

The difference between the two species was obvious when the cumulative percentage hatch of their eggs at various temperatures were plotted (Fig. 1). Many of *A. apicalis* eggs hatched at the relatively high temperatures of 20 and 25 °C. On the other hand, *T. asynamorus* showed a much lower hatchability at these temperatures, although a few eggs hatched before day 50 at 25 °C, and

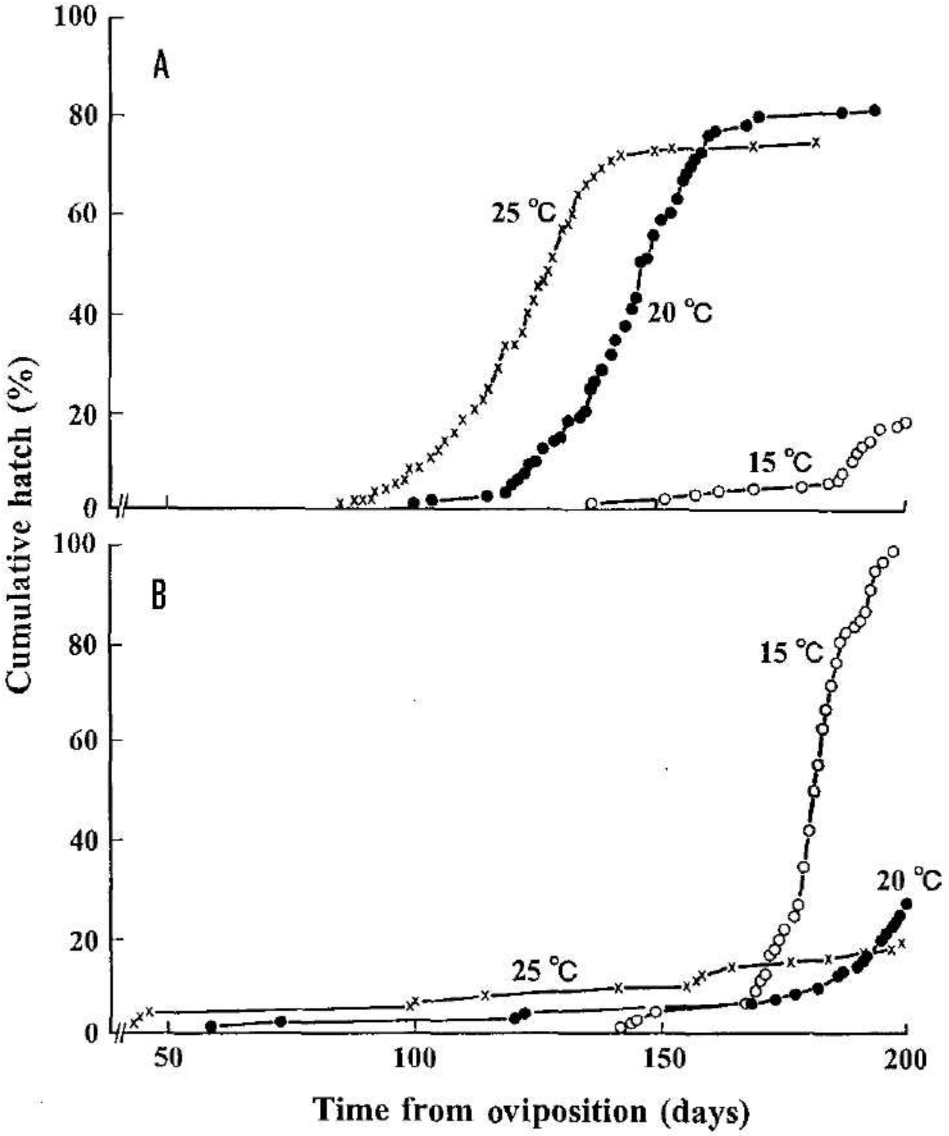

Fig. 1. Cumulative hatching curves for the eggs of (A) *Atachycines apicalis* (Brunner) and (B) *Tachycines asynamorus* Adelung kept at the constant temperatures indicated on each curve from immediately after oviposition.

Tab. 2. Fate of eggs of *Tachycines asynamorus* Adelung kept at constant temperatures for 250 days from deposition

Temper. (°C)	Number of eggs	With eyespots (%)	Hatched (%)	Hatchingtime*	Died (%)
4	111	0.0	0.0	—	8.1
7	106	0.0	0.0	—	6.6
10	119	79.0	0.0	—	12.6
15	115	80.9	73.0	181±11.0	13.0
20	118	67.0	50.0	225±47.7	6.8
25	170	15.3	12.4	159±69.0	20.6
30	163	11.3	4.9	108±50.5	18.4
35	120	0.0	0.0	—	100

*Mean ± SD days. The real means and SD's were much larger than shown except at 15°C as suggested by Fig. 1B.

day 80 at 20 °C. At 15 °C, in contrast, many eggs (70%) of *T. asynamorus* hatched but only a few (<20%) of *A. apicalis*. The higher ability to develop at lower temperatures in *T. asynamorus* was also indicated by its higher proportion (79%) of eggs reaching the eyespot stage at 10 °C than in *A. apicalis* (<22%) (Tabs 1, 2).

Although the eggs of the two species are clearly differ in their response to temperature, most of them require more than 100 days to hatch. The very long egg stage indicates they are in diapause.

Response to chilling

As usually found in diapausing insects, the hatchability and hatching time at 25 °C varied with the preceding exposure to lower temperatures (Masaki 1956, 1962, Masaki et al. 1979). In order to assess such effects in the camel crickets, we classified eggs based on their hatching time after chilling. For this purpose, the frequency distributions of hatching nymphs in all treatments are pooled as shown in Fig. 2. The two species show quite different distribution patterns.

In *A. apicalis*, some eggs hatched in weeks 2 to 17, and the rest survived but did not hatch before week 30. However, there was a depression in week 8 in the hatching distribution, so that we classified the eggs into three groups, (a) hatched in weeks 2 to 7, (b) hatched after week 7, and (c) persisted to week 30. This arbitrary classification was used to determine the changes in the egg's response to temperature. We cannot say that diapause was completely terminated in group 'a' eggs, because the range of from 2 to 7 weeks was unusually large for diapause-free development. Probably, most eggs in this group had to pass through the short final process of diapause before hatching, but in Fig. 2A, there is no clear demarcation to distinguish between diapause and diapause-free eggs.

In *T. asynamorus*, hatching reached a clear peak around week 5 and sharply dropped in week 7, after which low levels of hatching continued until week 30 when many viable eggs still remained (Fig. 2B). Although the hatching pattern was quite different in the two species, we used the same standard to classify eggs after chilling because three groups could be recognized in terms of the duration of egg stage in both species.

The response to chilling can thus be expressed as variations in the proportion of eggs of these categories (Figs 3, 4). The two species again show a clear difference in this response.

In *A. apicalis* (Fig. 3), chilling at 4 and 7 °C had no obvious effect on diapause termination, because the proportion of 'a' eggs was not increased by increasing duration of exposure before incubation at 25 °C. Chilling at 10 °C and higher temperatures was highly effective; the proportion of 'a' eggs increased with increasing duration of chilling and attained 100% after 15 weeks.

In *T. asynamorus* (Fig. 4), the lower temperatures (4, 7 and 10 °C) were more effective and 20 °C less effective in terminating diapause than in *A. apicalis*. In the 20 °C treatment, eggs in 'b' and 'c' groups were found in considerable proportions only after exposure for 15 weeks. Evidently, 20 °C is beyond the optimal range for diapause termination.

To summarize, *A. apicalis* requires a higher range of temperature for diapause termination than *T. asynamorus*. Temperatures from 10 to 20 °C were similarly effective in *A. apicalis*, but the most effective range was from 7 to 15 °C in *T.asynamorus*. Within the respective effective ranges of temperature, *T. asynamorus* terminated diapause faster than *A. apicalis*.

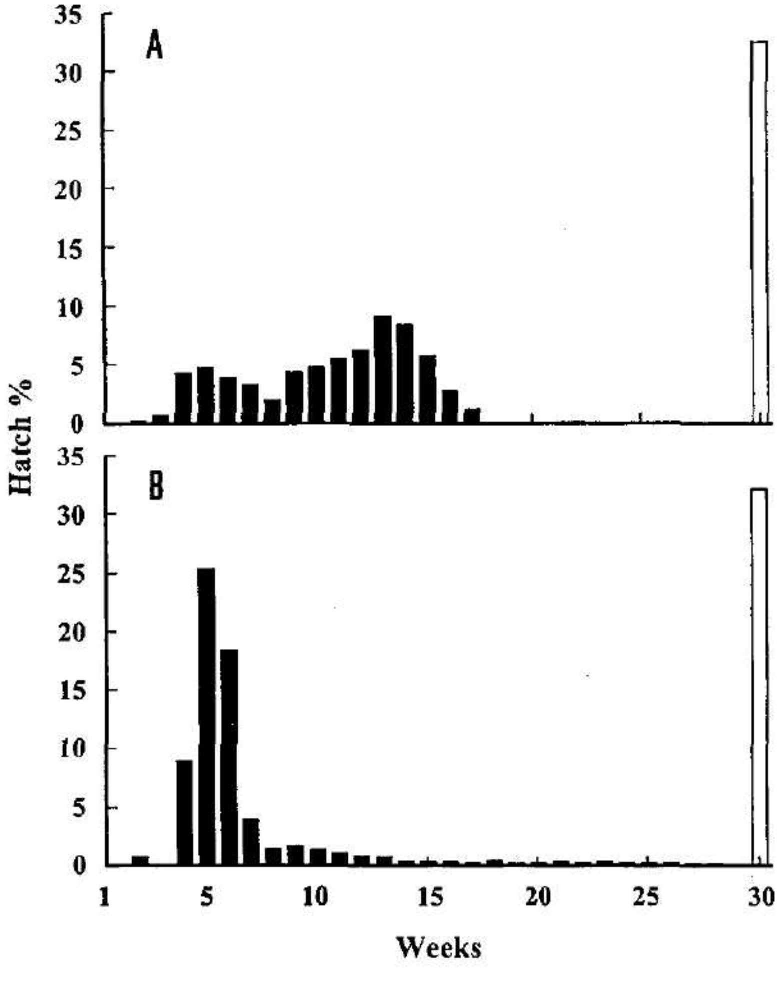

Fig. 2. Frequency distributions of hatching when eggs were kept at 25°C for 100 days after different periods of chilling at different temperatures. Data for different treatments are pooled to show three categories of eggs, 'a' hatched in 7 weeks, 'b' in 8 to 29 weeks, and 'c' remained unhatched for more than 29 weeks (open bars on the right end of abscissa). A, *Atachycines apicalis* (Brunner). B, *Tachycines asynamorus* Adelung.

Tab. 3. **Hatchability** of eggs of *T. asynamorus* kept at different temperatures for 100 days after chilling at 10°C for 8 weeks

Temper. (°C)	Number of eggs	Hatched (%)	Hatchingtime*	Rate of development	Died (%)
15	124	0.8	–	—	0.8
20	124	91.1	46±5.5	2.16	8.9
25	109	98.2	30±1.3	3.34	1.8
30	107	65.4	42±17.1	2.36	34.6

*Mean ± SD days.

Effect of incubation temperature after chilling

If diapause is terminated or its intensity is substantially reduced by chilling, the egg's response to temperature would be shifted to a pattern usually observed for morphogenetic processes. This inference could be tested only for *T. asynamorsus* because of the limited supply of *A. apicalis* eggs. Eggs were chilled at 10 °C for 8 weeks, then incubated at 4 different temperatures ranging from 15 to 30 °C and examined every day for 100 days.

The results are summarized in Tab. 3. The optimal temperature for postdiapause development seems to be close to 25 °C, at which the hatching time was shortest, the hatchability highest, and the mortality lowest. The next favourable was 20 °C, but 30 °C was too high for post-diapause development as indicated by increase in hatching time, its variance and mortality. At 15 °C, only a few eggs hatched within 100 days of observation, so that no accelerating effect on hatching was exerted by such a low temperature even after chilling. If the observation were continued much longer, the percentage hatching would have risen to the level of the eggs constantly kept at 20 or 25 °C.

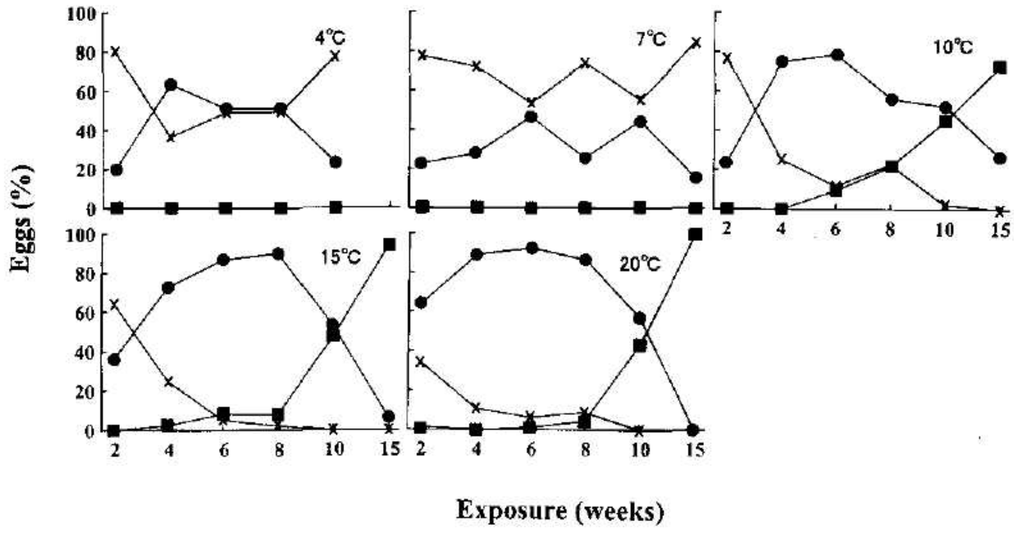

Fig. 3. Changes in the proportions of the three categories of eggs (see Fig. 2) as functions of chilling time in *Atachycines apicalis* (Brunner). The chilling temperature is indicated in each panel. Squares, circles and crosses indicate 'a', 'b', and 'c' eggs, respectively.

Seasonal succession of nymphal instars in *T. asynamorus*

The sample size obtained each month in the greenhouse varied from 7 to 20. The small sample sizes did not allow precise analysis, and therefore we roughly classified the trapped individuals into three size classes: large (adults and last instar nymphs), intermediate (middle instar nymphs) and small (1st and 2nd instar nymphs).

All size groups were found in each sample except in June, August and September, when 1st and 2nd instar nymphs were absent (Fig. 5). Whether this absence of young nymphs was due to a random error or real could not be determined because of the small sample sizes. The middle sized nymphs were most frequent except in October and November when there were more large sized nymphs.

Although there is little data, we can infer that large- and middle-sized nymphs overwinter because of their presence in early spring and late autumn. Early instars were more common in spring than in summer, probably because they hatched from diapause eggs laid by adults the previous summer and autumn. The appearance of a few very young nymphs in autumn might be attributed to sporadic hatching of eggs, which were laid at different times and diapaused for a long periods.

DISCUSSION

Temperature responses

Diapause in any stage of life cycle is generally characterized by an optimal range of temperature for its completion much lower than that for morphogenesis (Andrewartha 1952, Lees 1955). In association with this, the thermal coefficient $Q10$ for the rate of diapause completion deviates greatly from the normal range (2–3) for morphological development. Within a certain range of temperature, $Q10$

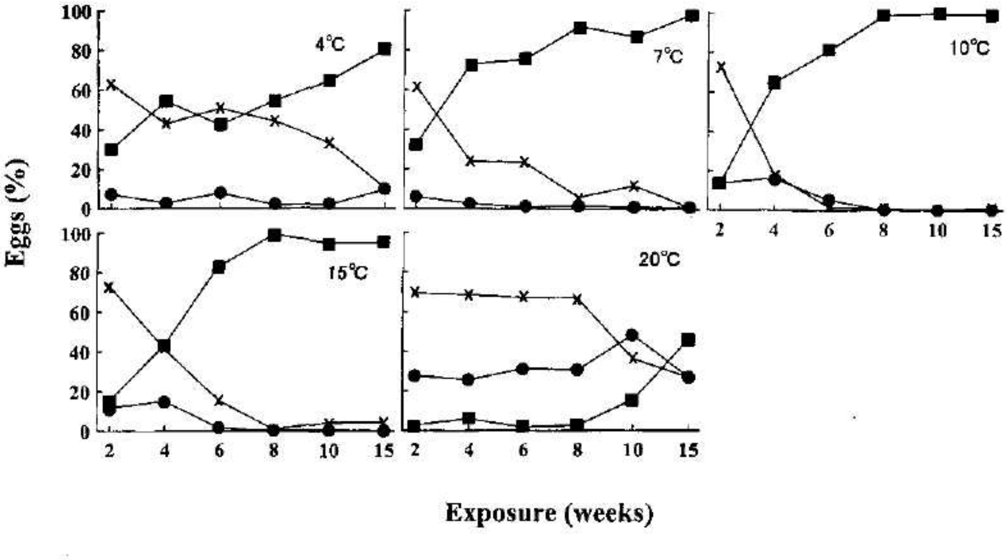

Fig. 4. Changes in the proportions of the three categories of eggs (see Fig. 2) as functions of chilling time in *Tachycines asynamorus* Adelung. The chilling temperature is indicated in each panel. Squares, circles and crosses indicate 'a', 'b' and 'c' eggs, respectively.

may take even a negative value as typically demonstrated by the leaf beetle *Atrachya menetriesi* Faldermann 1825 (Ando 1978) and *Locusta migratoria* Linnaeus 1758 (Ando 1993). However, the temperature relations of diapause development is highly variable among different species [for review, see Danks (1987)], and may change with time within a species and also in response to the preceding conditions (Masaki 1956, 1962, Maki & Ando 1967, Masaki et al. 1979, Ando 1993).

Hodek & Hodková (1988) extensively reviewed thermal relations of diapause and emphasized that diapause consists of different phases with different requirements, that chilling is not always necessary for the completion of diapause and that a high temperature may terminate diapause (see also Hodek 1999). These statements are supported by the responses of the two species of camel cricket described here. Eggs of *A. apicalis* can hatch at constant temperatures of 20 and 25 °C, taking on average more than 100 days. Probably, they would hatch also at 15 °C when kept more than 200 days (Fig. 1). A very few eggs of *T. asynamorus* hatched within a short time at 20 and 25 °C and the majority were retarded but started to hatch 150 days after deposition. At 15 °C, however, eggs hatched more or less synchronously, again showing that diapause is completed at this temperature without cold exposure.

We did not design experiments to delineate the multiple phases in diapause development, but the three different categories of eggs indicated by the polymodal distribution of hatching time after chilling (Fig. 2) and the changes over chilling time in their proportions (Figs 3 & 4) suggest that the eggs passed through at least three different physiological states during the process leading to diapause termination.

If there were only a single phase in diapause, there should appear only two groups of eggs on incubation at a high temperature (25 °C) after various lengths of chilling: those that terminated diapause, started morphogenesis immediately on incubation at a high temperature and hatched in

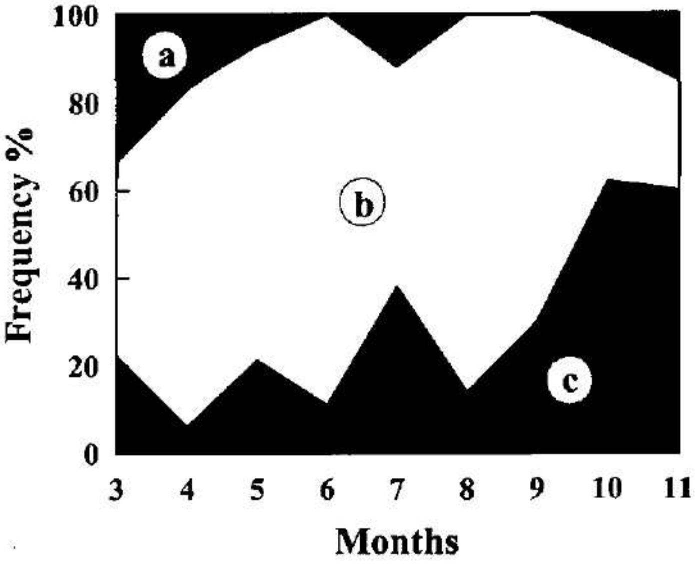

Fig. 5. Seasonal changes in instar compositions in *Tachycines asynamorus* Adelung in a greenhouse. (a) Small young nymphs (1st and 2nd instars); (b) middle-sized nymphs; (c) last instar nymphs and adults.

a short time, and those that still remained in diapause and failed to hatch. In our experiments, group 'a' is almost comparable to the former and group 'c' to the latter. Group 'b' suggests the existence of a phase in which the physiogenesis [in the sense used by Andrewartha (1951)] readily takes place either at the chilling temperature or at the high incubation temperature (cf. Masaki 1956). The three categories of eggs might represent different phases in diapause development.

Ecological relations

The eggs of the two species are considerably different in their response to temperature. One might infer that their ecological characteristics are reflected in this difference. Both species are found in more or less protected situations; *A. apicalis* lives in less protected conditions (forest floors, sewers, wells, caves) and might be exposed to lower temperatures in winter than *T. asynamorus*, which lives in human dwellings and greenhouses. However, diapause is effectively terminated by a moderate range of 10 to 20 °C in *A. apicalis* and by a lower range of 4 to 15 °C in *T. asynamorus*. Thus, the habitat conditions do not seem to be correlated with their different temperature responses. However, the diapause intensity as measured by the required length of chilling for termination within the optimal range of temperature is weaker in *T. asynamorus* than in *A. apicalis*. The weaker diapause might be related to the milder conditions in greenhouses.

However, the adaptive significance of egg diapause is not restricted to overwintering. For example, the hatching time mainly depends on the temperature responses during diapause, and there should be an optimal time for hatching for survival and reproduction. The temperature response is probably the only means to control hatching time in these camel crickets, because morphologically differentiated embryos are not detected in diapause eggs (K. Tani, unpublished observations). The eggs probably enter diapause before formation of the neuroendocrine system. This observation is in agreement with the description for the cave cricket *Dolichopoda linderi* (Dufour 1861) (Boudou-Saltet 1979, cited by Sbordoni et al. 1987). Probably, the eggs cannot respond to a photoperiodic cue. Moreover, there is no evidence for the maternal control of diapause in eggs laid in different seasons under different daylengths.

The higher temperature requirement would delay hatching in *A. apicalis* more than in *T. asynamorus* and this difference may affect the subsequent nymphal development and the population dynamics. Without more information on their life cycles and other aspects of ecology, we cannot infer the factors selecting for the species-specific temperature requirements for diapause termination in these camel crickets.

Phylogenetic constraints also might be involved in the moulding the life-cycle pattern (Di Russo et al. 1994). Most cavernicolous species of the Rhaphidophoridae undergo long periods of egg diapause and nymphal development, and show a wide range of age distribution in natural caves (Sbordoni et al. 1987, Di Russo et al. 1994). All those situations are similar to what we have found in our camel crickets. *T. asynamorus* is found as nymphs of various sizes in spring and autumn (Fig. 6) and the nymphal stage lasts more than five months at 25 °C (our unpublished data). *A. apicalis* is also observed in various instars before winter (Ito et al. 1977) and, at least in Hirosaki, we collected both small (probably 2nd instar) and large (last instar) nymphs soon after overwintering in April and May (unpublished data). These observations are evidence for overwintering by widely different instars.

Therefore, both species overwinter as eggs in the first year and as nymphs of variable instars or adults in the second year. Whether the overwintering nymphs and adults are in diapause or not, needs to be determined. It is almost certain, however, that they have biennial life cycles. They are also characterized by unsynchronized development. Various life stages occur in spring, summer and autumn (Fig. 5), situations ostensibly similar to homodynamic life cycles. This pattern could have been evolved in their more or less protected habitats. Exceptionally few eggs of *T. asynamorus* are able to hatch without diapause at 20 and 25 °C (Fig. 1). They might complete development within a year in the heated conditions of a greenhouse. To confirm this possibility, the effects of photoperiod on the incidence of such eggs as well as on the nymphal development should be studied.

The life cycle is an integrated system consisting of many coadapted subsystems. Selection pressures on the diapausing eggs will only be identified when we know more details of the ways of life of these species.

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We are honoured to be invited to participate in this special issue dedicated to Dr Ivo Hodek on the occasion of his 70th birthday. Dr Ivo Hodek has been inspiration to us through his many provocative papers on insect diapause.

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Does low rearing temperature increase diapause intensity in *Pyrrhocoris apterus*?

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Abstract. Diapause intensity in females of the bug *Pyrrhocoris apterus* (Linnaeus, 1758) is standardly measured as the oviposition delay after transfer to activating long day conditions (18L:6L) and constant temperature of 25 °C. We measured pre-oviposition period in bugs originally reared at short day, constant temperature of 20, 25, and 30°C. Before the transfer to activating conditions (long day, 25 °C), we exposed the bugs at 5 °C for 24 hours. The subsequent pre-oviposition period did not differ from the values measured without the chilling exposure. Thus, the changes of temperature do not function as a stimulus that might accelerate the diapause termination, and the measured values (16, 23, 20 days, respectively) represent the true diapause intensity. We conclude that low rearing temperature decrease diapause intensity in comparison with moderate temperature, but rearing at high temperature produces a moderate intensity.

Diapause intensity, pre-oviposition period, longevity, *Pyrrhocoris apterus*, Heteroptera

INTRODUCTION

The intensity of diapause changes over time during diapause development but may also differ between individuals / groups of organisms at the same early stage of diapause, e. g. in the same (short) time elapsed from the diapause induction. Such variability in diapause intensity can be attributed both to genetic and environmental factors. Photoperiod was revealed as one of the factors inducing this variation (Tauber et al. 1986, Danks 1987). Temperature is another source of variation in diapause intensity but the effect is ambiguous. In some species, higher temperatures during diapause induction and intensification produced more intense diapause than lower temperatures (Sieber & Benz 1980, Denlinger & Bradfield 1981). In others, diapause was more intense after rearing at lower temperature (Glitho et al. 1991, Principi et al. 1990).

The intensity of diapause has been defined as the time required under given conditions before some measure of diapause end is observed (Danks 1987). Thus, in adult females, the pre-oviposition period is often used to describe the intensity of diapause. Varjas & Sáringer (1998) suggested the level of oxygen consumption as a better criterion of diapause intensity.

Kalushkov et al. (2000) found differences in diapause intensity of the bug *Pyrrhocoris apterus* (Linnaeus, 1758) between several temperature regimes. Among other conditions, the pre-oviposition period was longer (22 or 23 days – two experimental series) after the induction at constant temperature of 25°C than after the induction at 20 °C (17 or 19 days). However, the authors doubt whether they really have measured the initial intensity of diapause. The conditions at which the pre-oviposition period was measured was the same in all the treatments (18L:6D, 25 °C). While in the first sample, reared at 25 °C, this represented no change, in the second sample (20 °C), it meant a notable increase of temperature. This increase might represent a stimulus that accelerated the following termination of diapause. Thus, the sample reared at lower temperature might have a higher initial intensity of diapause, but a shorter pre-oviposition period was measured after the stimulating change in temperature. This speculation was supported by a temporal high increase of oxygen consumption in this sample.

Our aim has been to check whether additional substantial changes in temperature will act as a stimulus accelerating the termination of diapause, and thus achieve in a justified opinion whether more intensive diapause is induced under higher or lower constant temperature in *P. apterus*.

MATERIAL AND METHODS

The animals were F2 generation offspring of adults of the bug *P. apterus* (Heteroptera: Pyrrhocoridae) collected near to České Budějovice (49° N, 14° E), South Bohemia. The larvae were reared under long day conditions (18L:6D), at 25 °C till 4th instar. They were subsequently placed into diapause inducing photoperiod (12L:12D), and three constant temperatures: 20, 25, and 30 °C. At those temperatures they completed larval development and spent four weeks of adult life. Then pairs were separated in Petri dishes (about 40 per treatment), and fresh mass was measured. The bugs were then transferred to 5°C for 24 hours. Then they were placed into diapause terminating conditions (18L:6D; 25 °C), provided with food and water.

The time to laying first eggs was recorded for each female. The percentage of ovipositing tested females, so called oviposition incidence, was counted from their initial number. Females were separated from males, fecundity was not counted, and only longevity was observed. Data were analysed using STATISTICA software (Statsoft 1997).

RESULTS

Pre-oviposition period

The oviposition incidence of females was high and similar (χ^2=0.06, df=2, NS) in all treatments (Tab. 1). The distribution of the duration of pre-oviposition period was positively skewed in all three treatments (χ^2-tests for normality; p=0.006, 0.03, 0.004). Thus, we show both means and medians (Tab. 1), and besides ANOVA (F=44, $p<10^{-6}$.) we used non-parametric comparative statistic: Kruskall-Wallis test showed significant differences between the treatments (χ^2=32, df=2, $p<10^{-4}$), and Mann-Whitney tests of all pairs of treatments were significant ($p<10^{-4}$).

The pre-oviposition period was longest in females induced to diapause at the moderate constant temperature of 25 °C (Tab. 1). The females reared during diapause inducing period at the lower constant temperature of 20 °C showed the shortest pre-oviposition period.

Longevity, fresh mass

The duration of life in adult stage was normally distributed in all three treatments (χ^2-test for normality; p=0.03, 0.14, 0.17). ANOVA showed significant differences (F=16, $p=10^{-6}$), and Tukey HSD test showed that longevity of females induced for diapause at 30 °C was much longer than that in the other two treatments. Within treatments, longevity was not correlated with pre-oviposition period.

The fresh mass (normally distributed) of diapausing females before the transfer from diapause inducing conditions at 20 °C and 25 °C was lower (ANOVA, $p=7.10^{-4}$, Tukey HSD test) than from 30 °C. The rank of the means corresponded to the rank of longevity. Within treatments, mass did not correlate either with longevity or pre-oviposition period.

DISCUSSION

Low temperature was generally been reported to increase the incidence of hibernation diapause of "long-day" insects (Danks 1987, Tauber et al. 1986). As diapause incidence is mostly linked to diapause intensity, one would expect that the action of low temperatures during induction would strengthen diapause. Such effect was often recorded (Glitho et al. 1991, Principi et al. 1990). How-

Tab. 1. Oviposition incidence (OI), pre-oviposition period, longevity, and fresh mass in females of *Pyrrhocoris apterus* reared at three different temperatures under short day photoperiod. K I and K II are the experimental series in Kalushkov et al. (2000)

	N	OI (%)	pre-oviposition (days) mean±SD	M-W	median	longevity (days) mean	mass (mg) mean
20 °C	34	91	15.8±3.4 a	D	15.0 a	109±31 a	59.5±5.6 a
25 °C	46	91	22.7±3.5 c	A	22.5 c	123±29 a	61.5±9.3 a
30 °C	40	98	20.2±2.2 b	B	19.0 b	146±26 b	69.3±6.6 b
tests		NS	$<10^{-6}$		$<10^{-4}$	10^{-6}	7.10^{-4}
K I 20 °C	31		16.9±4.1	CD	18.0		
K I 25 °C	41		21.8±3.2	AB	22.0		
K II 20 °C	31		19.1±3.5	BC	18.0		
K II 25 °C	31		22.9±4.3	AB	22.0		

Significantly different values of our three treatments according to Tukey's HSD test (means) or Mann-Whitney tests in all pairs (median) are indicated by lowercase letters. Different values of both our and Kalushkov's treatments according to multiple Mann-Whitney tests are indicated by uppercase letters. The significance level 0.05 was adjusted according to Bonferroni by the number of all pairs of values (21) to 0.0024.

ever, Kalushkov et al. (2000) found significantly longer pre-oviposition period in *P. apterus* reared at higher constant temperature. While rearing at 25°C was followed by pre-oviposition periods of 22 and 23 days (two series), rearing at 20 °C produced oviposion delay of only 17 and 19 days.

Such finding is not unique. In the codling moth, *Carpocapsa* (=*Laspeyresia*) *pomonella*, induction of larval diapause at short days and 19 or 21 °C resulted in a short photoperiodic activation period of 20–30 or 30–40 days, respectively. Induction at a higher temperature of 26°C was followed by much longer activation period of 70–80 days (Sieber & Benz 1980). The field observation in the Hessian fly, *Mayetiola destructor*, indicated that higher temperatures induced more intensive diapause (Wellso 1991). In the corn borer, *Ostrinia nubilalis*, a more intensive larval diapause was induced at 22 °C than at 19 °C (Beck 1989).

It might be suggested that the longer pre-oviposition period induced by higher temperature serves for synchronization with those individuals that completed their development later in the season and experienced lower temperature during diapause induction. While in some species the synchronization appears adaptive, in *P. apterus* such type of sychronization does not seem to be needed. Diapause development is completed in mid-winter (Hodek 1971a) and the insects have enough time for sychronization before the reproduction is started due to the appropriate temperature increase in spring (Hodek 1988). Thus, Kalushkov et al. (2000) assumed that the increase in temperature by 5 degrees at the transfer of females from diapause-inducing 20 °C to activation conditions might represent an important stimulus overriding the impact of initially deeper diapause. When the insects lived at 25 °C both at short and long photoperiod no such stimulus was perceived, and true initial value was measured.

In our experiments, we exposed the bugs at even stronger stimulus – a temporal (24 hours) decrease of temperature to 5 °C, and subsequent rapid warming up to the diapause terminating conditions (25 °C). If the stimulus hypothesis were right, we would expect that the chilling period had override the effect of transfer from 20 to 25 °C. We would expect the pre-oviposition periods in both treatments shorter than in the study by Kalushkov et al. (2000) due to the stimulus of increase of the temperature from 5 to 25 °C, and less difference between the two treatments due to temperature memory reset by chilling.

However, we found just opposite results. The pre-oviposition period of females reared at 25 °C in both series by Kalushkov et al. (2000), and in our experiments did not differ from each other (Tab. 1). The values of our 20 °C treatment did not differ at least from one of the series of Kalushkov et al., while all groups reared at 25 °C differed from all groups from 20 °C.

We conclude that diapausing bugs *P. apterus* have their intensity of diapause rather rigidly set up, and fixed in some type of physiological memory. This intensity is not easily changed by fluctuations of external temperature. It is not surprising, because ectothermic animals in the field conditions are usually exposed to unpredictable and great diurnal and longer-scale variations in temperature, which should not much change the diapause state. Although *P. apterus* possesses a behavioural mechanism to reduce such variations (Honěk & Šrámková 1976), it still should not be sensitive to them. Similarly, the bugs have similar developmental rate at alternating temperature (thermoperiod) as in corresponding constant temperature (Nováková & Nedvěd 1999).

We believe that pre-oviposition periods of *P. apterus* of all treatments measured in this and previous (Kalushkov et al. 2000) studies to be the true initial values of diapause intensity of the females. We conclude that lower (20 °C) rearing temperature during diapause induction produces lower diapause intensity than moderate temperature (25 °C). However, it applies only for limited range of temperatures. Rearing bugs at even higher temperature (30 °C) resulted in moderate diapause intensity.

An alternative explanation might be that the decrease of the temperature to 5 °C had an inhibiting effect on the bugs. It was demonstrated (Hodek 1971b) that short chilling induced diapause in long-day bugs. However, a role of low temperature in intensification of already induced diapause was not precisely measured. The inhibiting effect of the temperature decrease in our experiment should be of the same magnitude as the stimulating effect of the subsequent temperature increase. Such compensation of the two opposite stimuli would result in diapause intensity similar to the values achieved without such chilling. However, we would still expect a decrease of the difference between the two treatments, due to partial memory reset, not an increase as in our results.

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BOOK REVIEW

ODUM E. P.: **Ökologie. Grundlagen, Standorte, Anwendung.** Third substantially revised edition. Translated by J. Overbeck. Georg Thieme Verlag: Stuttgart, New York, 1999. XI+471 pages. Format 170×240 mm. Soft cover. Price DEM 79.00. ISBN 3-13-382303-5

The author is director of the Institute of Ecology at Athens, Georgia. The presented volume introduces the third German edition translated and updated by Professor Overbeck (Max Planck-Institut für Limnologie, Plön, Germany). This edition is based upon the English original **Basic Ecology** (1983 by Saunders College Publishing). As stated in the preface by the translator, the extraordinary rapid development in the field of scientific ecology in recent years made a thorough textual revision indispensable. Numerous new sections have been introduced, physiological and biochemical foundations of ecological functions have been taken into account. The list of references embraces now also newer European literature. The publication consists of 14 parts divided into particular chapters and subchapters.

The introductory part presents the relation of ecology to other sciences and its relevance to the human civilization, levels of organization of biological sciences and taxonomical groups in the framework of ecology, and particular ecological principles. Parts 2 through 4 are concerned with the ecosystems, the energy in ecological systems, and with the principles and conceptions of biochemical circuits. Parts 5 and 6 provide insights into conceptions of the limiting and regulatory factors and organization of the community. The most extensive part 7 on population ecology ensures comprehensive coverage of characteristic properties of populations, carrying capacity, population growth rate, natality, mortality, diverse types of fluctuation and population dispersal, diverse interactions, and more. Part 8 centres attention upon the species and the individual in ecosystems. Analyzed are the habitats and ecological niches, ecological equivalence, character displacement: sympatry and allopatry, natural selection, artificial selection, biological clock, basic behaviour pattern: ethology and behavioural ecology, regulatory, compensatory and social behaviour.

Part 9 focuses on development and evolution of ecosystems, namely on the development strategy and the bioenergy in ecosystems, allogenous and autogenous successions, food chains and webs, diversity and succession, nutrient cycling, climax, human ecology, compartment model, evolution and coevolution, and group selection. Part 10 is devoted to the mathematical modelling in the ecology. Parts 11 through 13 encompass the limnology, marine and estuarine ecology. Part 14 examines the terrestrial environment, in particular the terrestrial biota and biogeographical regions, general structure and distribution of terrestrial communities, and most important biomes. Textual parts are concluded by English-German and German-English glossaries of key terms. The volume is illustrated with 222 colour-enhanced figures: line drawings present schemes and diagrams of environmental processes, material cycles and nutrient cycling, diverse forms of organisms, landscape profiles and cross-sections, geographical maps; black-and-white photographs demonstrate various plant and animal populations and communities in their natural environment. In addition, 62 tabular overviews summarize miscellaneous ecological, biological, chemical and physical data.

The "Odum" is a classic among the textbooks of ecology. It offers in a comprehensive and attractive form complete overview of the environmental science reflecting new developments – with special reference to the ecology of humans.

Jindřich Jíra

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The effect of hibernation on the seasonal variations in adult body size and sex ratio of the polymorphic ladybird beetle *Harmonia axyridis*: the role of thermal melanism

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Abstract. Seasonal variations in adult body size in *Harmonia axyridis* (Pallas, 1773) were analysed over four consecutive generations according to sex and state of melanism. In males, there was a difference in body size in the four generations. The difference was significant in melanics, and marginally significant in non-melanics. However, in females, a significant difference in body size was observed only in melanics. Males in summer 1987 were significantly larger than those in 1988 in both melanics and non-melanics. Males in spring were significantly larger than those in summer only in melanics in 1988 and males in summer were significantly larger than those in spring only in non-melanics in 1987. On the contrary, in females in 1987, melanics in spring were significantly smaller than those in summer. Furthermore, no significant difference was observed in non-melanic females in the four generations. The sex ratio in melanics was significantly female biased in spring 1988. While, the sex ratio in non-melanics was significantly female-biased in spring 1987 and summer 1988. The mean temperature during the hibernation period before spring 1988 was lower than that before spring 1987 and for the average for the same period for 1966 to 1995, and the difference between the minimum and maximum temperatures before spring 1988 was larger than that in 1987 and the long term average for this period (1966 to 1995). These results suggested that sex- and morph-related difference in cold tolerance during hibernation may affected the variations in body size and the sex ratio of the spring generation of *H. axyridis*.

Morph-related death, sex, size difference, winter mortality, Coleoptera, Coccinellidae, *Harmonia axyridis*

INTRODUCTION

In coccinellids, the combined effects of fluctuating temperature and food condition in the larval stages are considered to cause the variation of adult body size in a natural population (Hodek & Honěk 1996). Diapausing insects typically show an increased fat content (Lees 1955, Hodek & Čerkasov 1963, 1965, Beck 1968, Tauber et al. 1986, Danks 1987). Furthermore, marked enlargement of the fat body is a conspicuous feature of diapausing coccinellids in both males and females (Hodek & Honěk 1996). Moreover, in many coccinellid species, females had a higher absolute fat content than males (Hodek & Čerkasov 1963) Glycogen reserves are also accumulated during prediapause (Hodek & Honěk 1996). Furthermore, in *Semiadalia undecimnotata* (Schneider, 1792), a markedly high glycogen content was found in the female (Hodek & Čerkasov 1963). In coccinellids, females are generally larger than males. Thus, females may have an advantage over males in hibernation. In fact, Ohgushi (1986) showed that sex- and/or size- dependent mortality resulted in larger adults and a higher proportion of females in the overwintering generation in the herbivorous ladybird beetle *Henosepilachna niponica* (Lewis, 1896).

Another factor which influences on survivorship during hibernation may be melanism of elytra in coccinellids. In the polymorphic ladybird beetle *Adalia bipunctata* Linnaeus, 1758), the industrial and climatic effects may affect frequency of morphs through a common melanism consisting of balanced selection (e.g., Tomofžeff-Ressovsky 1940, Creed 1966), but different results were obtained in different areas (e.g., Honěk 1975). While, thermal melanism results in earlier reproductive activities of melanic morphs (Brakefield 1984). Furthermore, Brakefield (1985) showed that intense selection favouring melanic morphs occurred during hibernation; the relative fitness of non-melanics was 45 % smaller than that of melanics. However, laboratory experiments with the hibernating beetles found no difference in survivorship or rate of weight loss between starved non-melanics and melanics in temperature regimes with and without periods of adult activity (Brakefield 1985). There may be variations of mortality and adult size among each morph after hibernation in polymorphic ladybird beetles if the colour of elytra is related with thermal absorption. However, the sex- and morph-related differentiation in mortality and size variation of adults after hibernation in a polymorphic ladybird beetle is less well documented.

In this study I analysed the distribution patterns in body size and the sex ratio in melanic and non-melanic morph in the ladybird beetle Harmonia axyridis to clarify the effect of hibernation.

MATERIALS AND METHOD

The ladybird beetle

The ladybird beetle *Harmonia axyridis* (Pallas 177 shows a wide natural distribution in north-eastern Asia (c.f. Sasaji 1971). *H. axyridis* typically has four elytral colour morphs: succinea (h), axyridis (h^X), spectabilis (h^S), and conspicua (h^C) (see Komai 1956). The genes controlling colour morphs form multiple-allelic series, with the dominance order of h<hX <hS < hC (Hosino 1933, 1936, Tan & Li 1934, Tan 1949). The beetles with black elytra (axyridis, spectabilis, and conspicua) were regarded as melanics and those with orange elytra (succinea) as non-melanics (see Osawa & Nishida 1992). In the study area, the adults of the second and/or third generations aggregate at hibernation sites in early November (Obata 1986) and the adults terminate hibernation in late March.

A field observation

All the research was done at the Botanical Garden , Kyoto University (35° 02' N, 135° 47' E)(see Osawa 1993, 2000). I chose 20 sites in 1987 and 24 in 1988 to do the research of the beetles. *H. axyridis* adults were captured and individually marked by four dots with quick drying paint and also by drilling four tiny holes with an insect pine. Every day from early April to late July in 1987, and 1988, the marked beetles were released at the same host plant where they were caught after recording the sex and colour of morph. The body size (total body length to the nearest 0.01 mm) was measured for newly caught beetles in 1987 and 1988. Individuals of the summer generation (= the first generation) were distinguished from those of the spring generation (= overwintering generation) on the basis of pale and soft elytra of newly emerged adults (Brakefield 1984, Osawa & Nishida 1992). The data of the newly captured beetles (n= 1062) were used for the following analysis.

Meteorological data

For analysis of the temperature to body size and the sex ratio in *H. axyridis*, monthly meteorological data (mean, minimal, and maximal temperature and relative humidity at daily basis) from November 96 to December 1988 and that from 1966 to 1995 (mean, minimal, and maximal temperature and relative humidity at monthly basis) in the Forest Experimental Station in Kyoto University (35° 02' N, 135° 47' E), which is located at the same campus of the Botanical Garden, were used (Kyoto University Forests 1993, 1998).

Analysis of data

The distribution patterns of body size of the beetles were analysed by distribution procedure, body size of the adult beetles by Kruskal-Wallis nonparametric test, and sex ratio of the populations by Chi-square test (SAS Institute 1995).

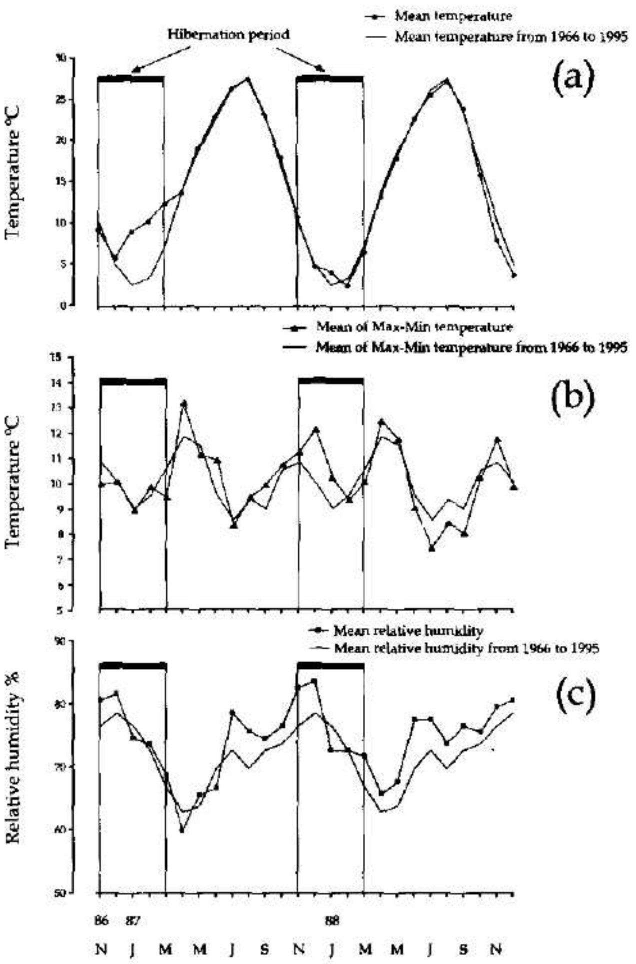

Fig. 1. Mean temperature (a), the difference between maximal and minimal temperature (b), and mean relative humidity (c) at the research site from November 1986 to December 1988. The mean values from 1966 to 1995 are also shown.

RESULTS

Meteorology at the research site

Figure 1 shows the mean, minimal, and maximal temperature, and mean relative humidity from November 1996 to December 1988 and those from 1966 to 1995. The mean temperature for the season of hibernation in *Harmonia axyridis* before spring 1987 was much higher than that before spring 1988 (Fig. 1a). Moreover, the mean temperature in 1987 was higher than that from 1966 to 1995, while the mean temperature in 1988 was higher in January but lower in February, compared with that from 1966 to 1995 (Fig. 1a). The mean difference in minimal and maximal temperature during the season of hibernation in *H. axyridis* before 1988 spring was larger than that before 1987 spring (Fig. 1b). Apart from temperature, the difference in mean relative humidity during hibernation between the two years was not clear, although in 1988 the mean relative humidity in March was much higher than that in 1987 and that from 1966 to 1995 (Fig. 1c).

Size difference and its distribution patterns in *H. axyridis* according to sex and state of melanism

Fig. 2 shows the body size in melanics and non-melanics in males and females in *H. axyridis*. In melanic males, there was a significant difference in body size with the year and generation (df=3, $\chi^2=8.547$, P=0.0360). In non-melanic males, the difference in body size through the four generations was marginally significant (df=3, $\chi^2=7.792$, P=0.0505) . In melanic females, there was also a significant difference in body size among year and generation (df=3, $\chi^2=12.343$, P=0.0063). However, in non-melanic females, the difference was not significant (df=3, $\chi^2=2.996$, P=0.3923). In melanic males, no significant difference was observed in body size between the spring and summer generations in 1987 ($\chi^2=1.268$, P=0.2601). However, the difference was significant in 1988 ($\chi^2=4.583$, P=0.0323). In spring, the difference in body size between the populations in 1987 and 1988 was not significant ($\chi^2=2.0612$, P=0.1511), while in summer, the difference was significant ($\chi^2=6.332$, P=0.0119). In non-melanic males, a significant difference in body size was observed between the spring and summer generations in 1987 ($\chi^2=6.169$, P=0.0130). However, the difference was not significant in 1988 ($\chi^2=0.485$, P=0.4861). In spring, the difference in body size between the populations in 1987 and 1988 was also not significant ($\chi^2=0.570$, P=0.4502). However, in summer the difference was significant ($\chi^2=4.670$, P=0.0307). In melanic females, a significant difference in body size was observed between the spring and summer generations in 1987 ($\chi^2=7.555$, P=0.0060), while the difference was not significant in 1988 ($\chi^2=0.007$, P=0.9347). In spring, the difference in body size between the populations in 1987 and 1988 was significant ($\chi^2=8.915$, P=0.0028). However, in summer, the difference was not significant ($\chi^2=0.009$, P=0.9242). In non-melanic females, no significant difference in body size was observed between the spring and summer generations in 1987 and 1988 ($\chi^2=0.148$, P=0.7009, $\chi^2=0.918$, P=0.3381, respectively). Moreover, the difference in body size between the populations in 1987 and 1988 was also not significant in the spring and summer generations ($\chi^2=0.020$, P=0.8880, $\chi^2=1.943$, P=0.1633, respectively).

The difference in the state of melanism did not significantly affect body size in males and females (combined data in 1987 and 1988) ($\chi^2=0.424$, P=0.5151, $\chi^2=0.004$, P=0.9516, respectively). Moreover, no significant difference in body size between melanics and non-melanics was observed between the spring and summer generations in males and females (combined data in 1987 and 1988)(spring males; $\chi^2=1.919$, P=0.1660, summer males; $\chi^2=0.105$, P=0.7463, spring females; $\chi^2=1.784$, P=0.1816, summer females; $\chi^2=1.112$, P=0.2916).

None of the distribution patterns in body size in 1987 was significantly different from the normal distribution (Shapiro-Wilk W test, P>0.05)(Fig. 3). However, in 1988 the distribution pattern in body size was significantly different from the normal distribution in melanic females in spring, and melanic males and females in summer, with a low proportion of smaller beetles and a high proportion of larger ones (Shapiro-Wilk W test: W=0.953, P<0.0047, W=0.962, P<0.0101, W=0.966, P<0.0150, respectively)(Fig. 3).

Sex ratio in males and females in melanics and non-melanics

Figure 4 shows the sex ratio in H. axyridis in 1987 and 1988. The sex ratio in melanics was significantly different during the four generations (df=3, χ^2=8.157, P=0.0429); the sex ratio was significantly

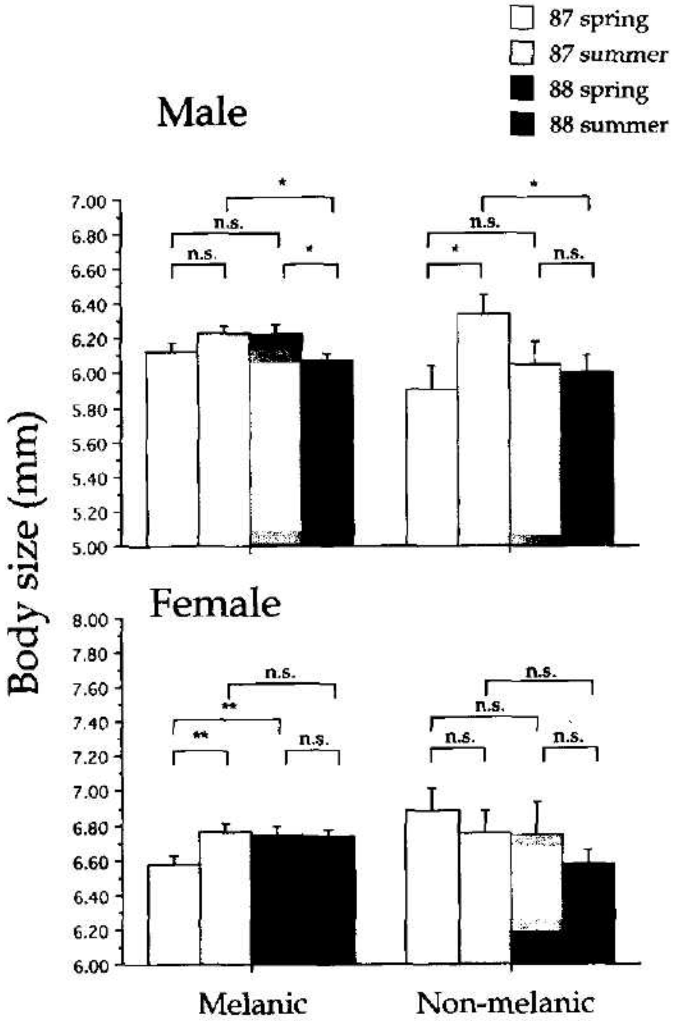

Fig. 2. Adult body size of *Harmonia axyridis* Pallas in melanics and non-melanics in spring and summer. Vertical lines indicate S.E. Asterisks (*), double asterisks (**), and n.s. indicate statistical difference from the Kruskal-Wallis nonparametric test at P=0.05, P=0.01, and P>0.05 level of significance, respectively.

biased toward female only in spring 1988 (χ^2=7.968, P=0.0048), while no significant bias in sex was observed in the other generations (spring 1987; χ^2=0.843, P=0.3585, summer 1987; χ^2=0.308, P=0.5789, summer 1988; χ^2=0.859, P=0.3539). In 1987, the sex ratio in melanics showed no significant difference between the spring and summer generations (χ^2=0.205 P=0.6510). However, in 1988, the sex ratio in spring was significantly different from that in 1988 (χ^2=5.825, P=0.0158). In spring, the sex ratio in melanics in 1987 was significantly different from that in 1988 (χ^2=4.835, P=0.0279). However, in summer, the sex ratio in 1987 was not significantly different from that in 1988 (χ^2=0.132, P=0.7163). A significantly biased sex ratio was also observed in non-melanics during the four generations (df=3, χ^2=10.241, P=0.0166); the sex ratio was significantly biased toward female in spring 1987 and in summer 1988 (χ^2=4.218, P=0.0400, χ^2=5.048, P=0.0247, respectively), while no significant bias in sex was observed in the other generations (summer in 1987; χ^2=0.580, P=0.4460, spring in 1988; χ^2=0.589, P=0.4426). In 1987, the sex ratio in non-melanics showed no significant difference between the spring and summer generations (χ^2=2.400 P=0.1213). However, in 1988, the sex ratio in spring was significantly different from that in summer (χ^2=7.572, P=0.0059). In spring, the sex ratio in non-melanics in 1987 was significantly different from that in 1988 (χ^2=7.239, P=0.0071). However, in summer, the sex ratio in 1987 was not significantly different from that in 1988 (χ^2=2.321, P=0.1276).

DISCUSSION

Morph- and size- related death during hibernation

This study showed that there was a significant difference in body size during the four generations in melanic males. Moreover, the difference was marginally significant in non-melanic males. In females, however, a significant difference in body size through four generations was observed only in melanics. These results suggest that sex- and morph-related selective selection is involved in seasonal variations in body size in *Harmonia axyridis*.

In *H. axyridis*, non-random mating plays an important role in seasonal variation in colour polymorphism; melanic and non-melanic females preferentially choose non-melanic males in spring, but non-melanics are less successful at mating than melanics in summer (Osawa & Nishida 1992). Moreover, it is known that large males have an advantage over small males in mating (Osawa & Nishida 1992, Ueno et. al. 1998). Therefore, morph-related sexual selection may be also involved in the seasonal variations in body size, especially in males.

The winter before spring 1987, it was rather warm and the difference between the minimal and maximal temperature was small, while the winter before spring 1988 it was rather cold and the difference was large, although the difference in relative humidity between the two years was small. In coccinellids, females have a higher fat content and glycogen reserves than males (Hodek & Čerkasov 1963, Hodek & Honěk 1996). Additionally, females are generally larger than males. Therefore, the physiological mechanisms against cold tolerance may be involved in the variations of body size in spring in males and females. This study showed that melanic females in the spring generation in 1988 were significantly larger than those in 1987. This suggests that, al least in melanic females, size- related death occurred before spring 1988; small melanic females may die during the hibernation. The result that the distribution pattern in body size in melanic females in spring 1988 was significantly different from the normal distribution may also support this phenomenon. In melanic and non-melanic males in the spring generation, the body size in 1987 was not significantly different from that in 1988. Moreover, the four distribution patterns in body size in melanic and non-melanic males in spring were not significantly different from the normal distribution. However, the sex ratio was significantly biased toward female in melanic males in spring 1988, and in non-melanic males in spring 1987. These results suggest that mortality is unrelated to size in males; males during

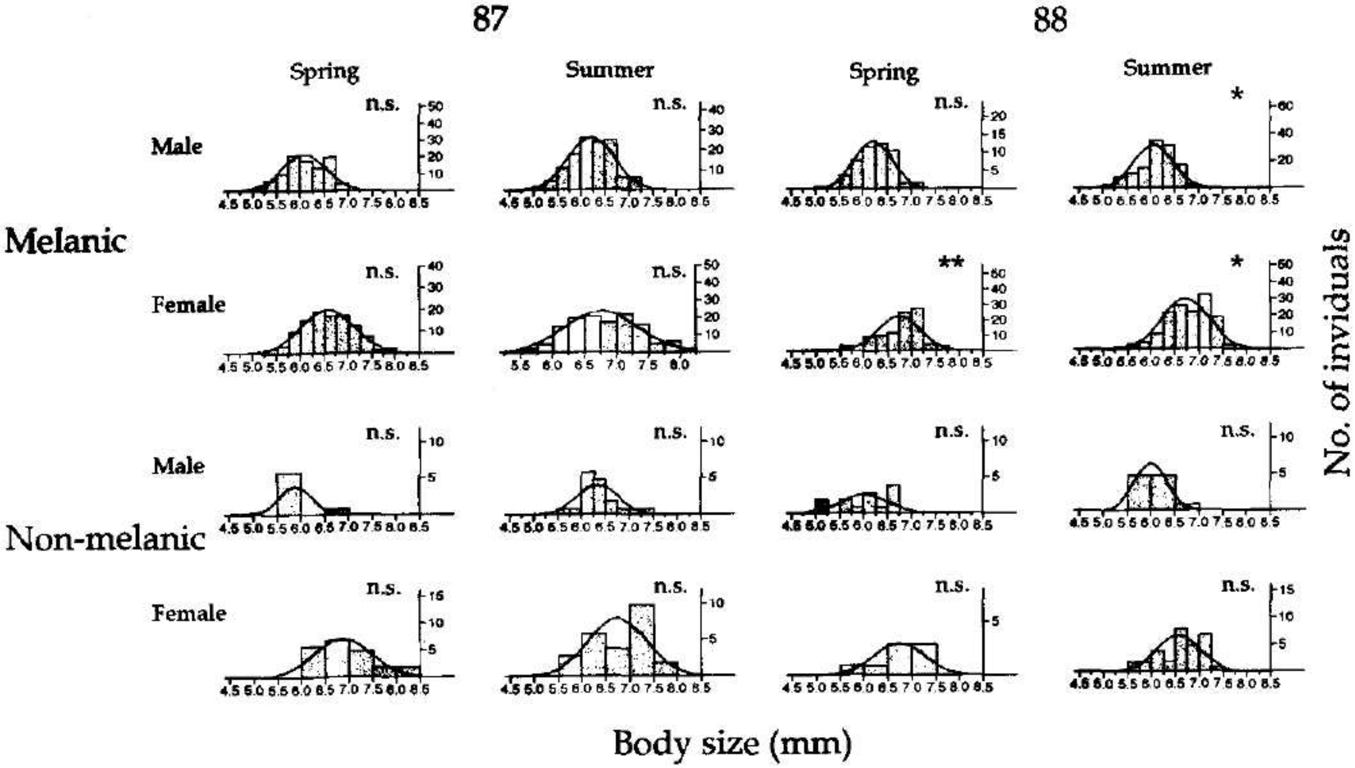

Fig. 3. The distribution patterns in adult body size in melanics and non-melanics of males and females in *Harmonia axyridis* Pallas. The curved line in each figure shows the normal curve. Asterisks (*), double asterisks (**), and n.s. indicate statistical difference from the normal distribution by the Shapiro-Wilk W test at P=0.05, P=0.01, and P>0.05 level of significance, respectively.

hibernation may die regardless of their size, higher mortality in melanic males during a cold winter and higher mortality in non-melanic males during a warm winter, resulting in biased sex ratio toward female in the spring generations. In non-melanic females, the body size was not significantly different during the four generations, showing that size-related death may not occur in non-melanic females.

Size difference in summer generation

This study showed that body size in both melanic and non-melanic males in the summer generation was significantly larger in 1987 than in 1988, while there was no significant difference in body size in the females. In coccinellids, the mechanism determining body size is rather complicated; combined effects of fluctuating temperature and intermittent starvation give rise to a greater variation of body size in natural populations (Hodek & Honěk 1996). The differences in the mean, maximal and minimal temperatures from April to June between 1987 and 1988 were rather small in the field. Furthermore, there was no significant difference in size between the melanic and non-melanic females. These results suggested that temperature in the developmental period may not be related with the size variations of the summer generation in *H. axyridis* between 1987 and 1988. The mortality rate (egg to adult) in the *H. axyridis* population in 1988 was higher than that in 1987; it was 99.01% in 1988, 98.32 % in 1987 (Osawa 1993). Moreover, the suitable aphid density for the food of *H. axyridis* in 1988 was lower than that in 1987 (Osawa 2000). However, there was no significant difference in adult mortality among the four morphs in the field (Osawa & Nishida 1992). Considering these results with the meteorological data, the low aphid density in spring 1988 may have been caused by the low temperature before spring 1988, resulting in higher mortality and lower develop-

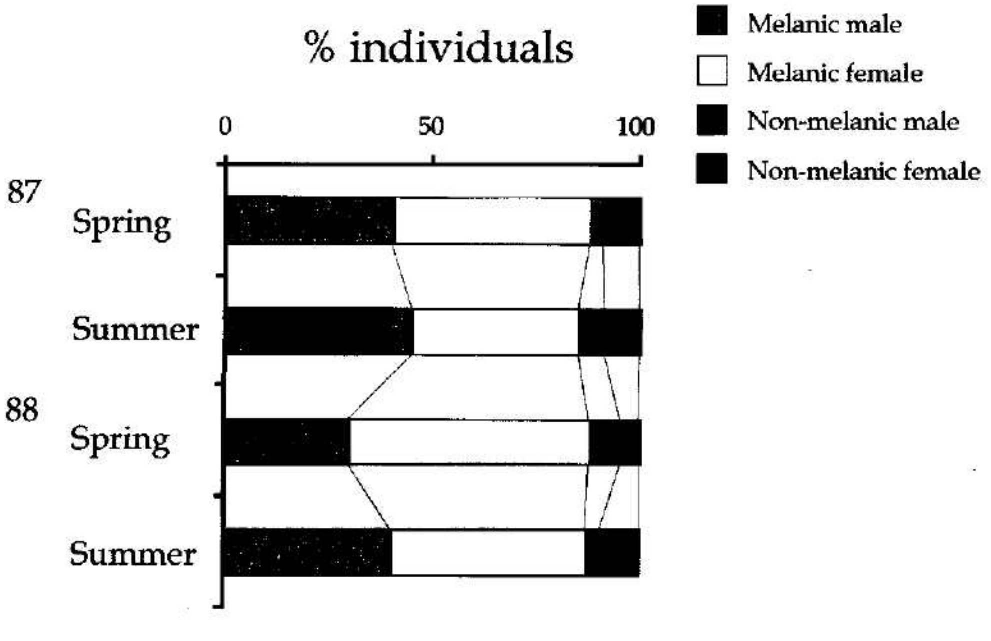

Fig. 4. The sex ratio in melanics and non-melanics in *Harmonia axyridis* Pallas.

ment in H. axyridis in summer 1988. This may be supported by the result that body size (= the length *of elytra) positively increased in relation to the amount of food in the aphidophagous ladybird* beetle *Menochilus sexmaculatus* (Okamoto 1978). In fact, the beetles in the spring generation tended to be smaller in 1988 than in 1987 in both males and females and both in melanics and non-melanic, although in females the differences were not significant. Therefore, intense starvation during the developmental period in the larvae might have influenced the body size in H. axyridis in summer 1988, in a manner that the effect on body size was stronger in males than in females.

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